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The reproductive ecology of Double-crested Cormorants in southern Alberta

by

Ⓒ Steven Henry Brechtel

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
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Fred C. Zwickel

L. C. H. Wang

Date March 30, 1983

Dedication

For Gail . . .

Without your patience, support and hard work this thesis could never have been completed.

Abstract

The reproductive parameters and chronology of Double-crested Cormorants in southern Alberta were studied between 1978 and 1980. Detailed reproductive data were collected from marked nests and eggs during weekly or twice-weekly visits to 2 colonies in 1979 and 3 colonies in 1980. In addition, more general data were collected by monthly visits to most southern Alberta colonies during all years of the study.

Earliest cormorants returned to their nesting islands during late April. Adults were observed earlier than yearlings or two year olds and males appeared to return, in greater numbers, earlier than females. Nest initiation date, as defined by the appearance of the first egg in a nest, averaged May 10. Egg loss occurred prior to clutch completion in 17% (n = 85) at the nests studied. Mean clutch size was 3.53, with the modal clutch of 4 being more common than all other sizes combined. The physical dimensions of 448 eggs were documented. The ultimate fates of 1657 marked eggs were determined. The average in-nest period for eggs which hatched was 27.2 days. The mean hatching success for 495 marked nests was 59%, resulting in an average brood size of 2.16 (range = 1 to 5). Mean fledging success, defined as chick survival to 18 days, was 73%, resulting in an average of 1.58 fledglings per nest. The weight growth and within brood survival of 64 marked nestlings were examined. From a sample of 3143 banded fledglings, minimum post fledging on-colony mortality was estimated at 4.8%. The pattern of fall departure was recorded and suggested that the Newell colony was used as a pre-migratory staging area. The reproductive parameters of renesting birds were examined separately and were found to be lower than those from first nests.

Variation in these reproductive parameters was examined among several temporal categories. In general, both reproductive output and success decreased as the season progressed and cormorants nesting in the later, cooler year of 1979 were less successful than those nesting in 1980.

Spatial variation in reproductive parameters was also examined. Newer, smaller colonies had greater reproductive output but generally equivalent reproductive success than older, larger colonies. Breeding pairs preferentially selected central over peripheral nest sites and had greater success at these central locations. Nest height increased with nest age. All measures of reproductive output were numerically greater in high (> 30 cm) nests than in either medium (15–30 cm) or low (0–15 cm) nests, and nesting success was significantly greater in high nests. Cormorants preferred using nest sites which were two or more years old and had greater reproductive output and success at these locations.

Cormorant reaction to, and the reproductive consequences of, human disturbance at the colony site were also examined. Breeding birds were most attached to their nests during the peak of the reproductive season and less attached both early and late in the year. Neither annual nor between-colony variation in reproductive success could be clearly attributed to either habituation or variation in the intensity of research disturbance. Reproductive output was, however, greater in the more frequently disturbed colonies.

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I. INTRODUCTION

Background and Objectives

In 1977 the Alberta Fish and Wildlife Division began the preparation of a Species Management Plan for the Alberta population of Double-crested Cormorants (*Phalacrocorax auritus auritus*). While carrying out the preliminary literature review for this program, I became aware that there were not sufficient data on either the reproductive ecology or population status of this species in Alberta to develop effective management programs. Due, in part, to this lack of population data and in response to a demonstrated need for habitat and management protection, Double-crested Cormorants were declared to be 'endangered species' under the Alberta Wildlife Act in November of 1977. In retrospect, this designation may be judged as overprotective, but at the time it encouraged the immediate protection and management of threatened nesting colonies in several areas of the province. Most important of these was Pelican Island in Lake Newell. In 1977 this single island supported between 30 and 40% of the breeding cormorants in Alberta. Without the immediate protection which was provided under this legislation, rising water levels resulting from increased irrigation storage would have destroyed this nesting island.

An additional value implicit in this designation, was that the provincial government recognized the need for a much more active management program for this species. In order to fulfill this responsibility, a more complete understanding of the biology and status of the Alberta cormorant population was required. The Alberta Fish and Wildlife Division therefore agreed to support the research program which I proposed in the winter of 1978.

The overall intent of this study was to provide a more comprehensive understanding of the reproductive ecology, history and status of Double-crested Cormorants in Alberta, upon which a comprehensive management program could be built. Much of the data collected on history, population status and trends, and general reproductive parameters has already been applied to the final production of a Species Management Plan for cormorants in Alberta (Brechtel, 1981). The objective of this thesis is to report in more detail on several specific aspects of the reproductive ecology of Double-crested Cormorants in southern Alberta. Three major topics are addressed:

1) A detailed documentation of the reproductive output, success, and chronology of southern Alberta cormorants,

2) an examination of how these reproductive parameters vary between years, colony types and nest site characteristics, and

3) a description of this species' response to human disturbance at the colony site, and the effect this disturbance has on reproductive parameters.

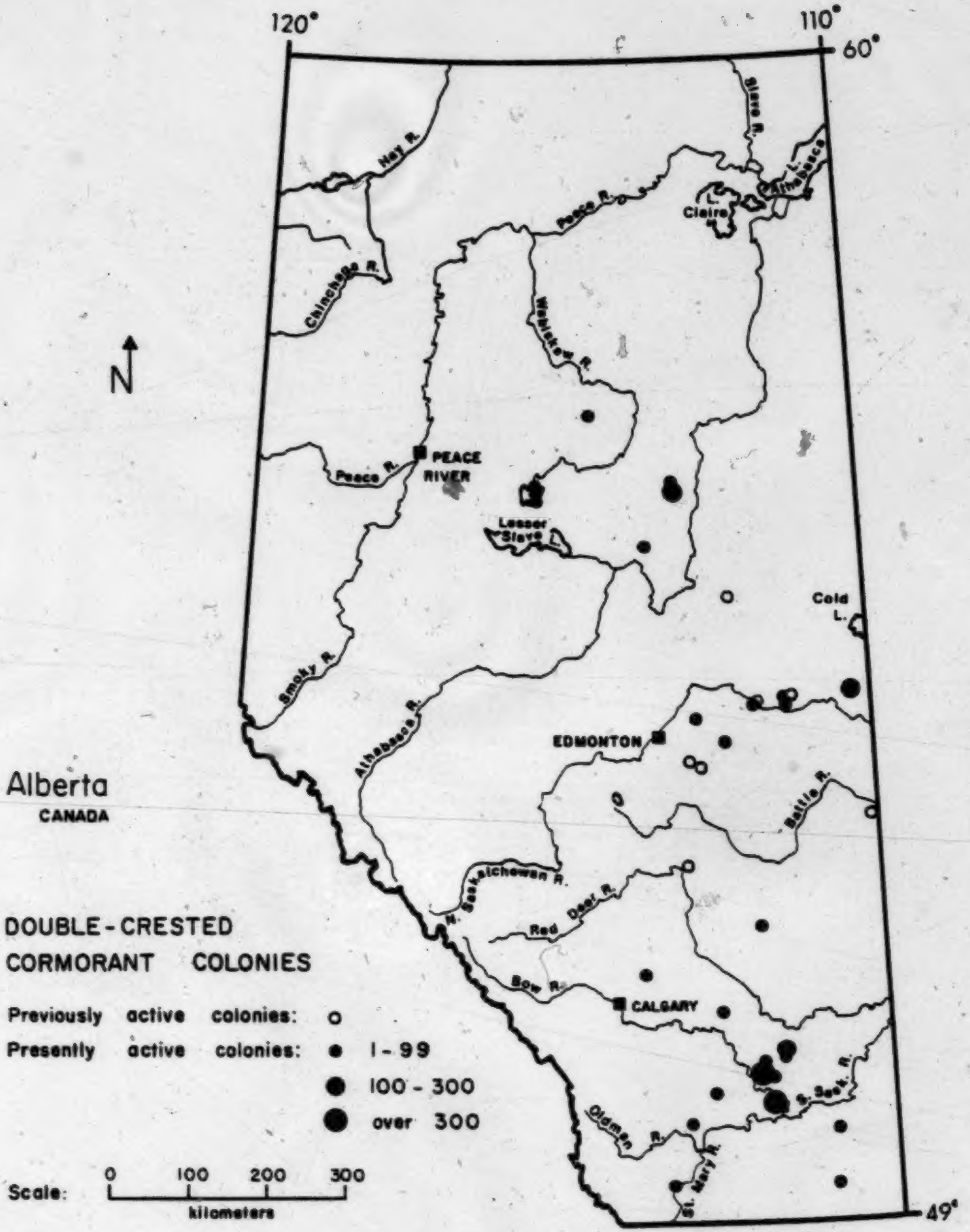
Several additional research topics, including food habits, migration, survival and subadult colony fidelity will be published elsewhere (Brechtel and Lewin, in prep.).

The Species

The Double-crested Cormorant is the most widely distributed Nearctic member of the family *Phalacrocoracidae*. It breeds throughout much of North America, from the prairie provinces east to Newfoundland, south to Mexico and the Bahamas. It also breeds in Alaska and down the Pacific coast from Vancouver Island to the Baja peninsula. Of the four recognized subspecies, only *P. auritus auritus* is found in Alberta (Palmer 1962).

Double-crested Cormorants are the only North American cormorant species which breeds on inland fresh water. They reach both the northern and western limits of the mid-continent breeding range in Alberta. In Alberta, colonies are found in the prairie, parkland and southern boreal forest regions (Figure 1). Their known range has expanded in recent years, with new colonies being located in both northern and southern areas of the province. In 1980 the provincial breeding population was estimated at approximately 4,600 breeding adults, with the total population, including non-breeding and subadult birds, being 1.5 to 2 times this number (Brechtel, 1981).

Although at least 6 colonies are known to have been abandoned in Alberta prior to 1980, there has been a drastic increase in both the number and size of cormorant colonies in the past 13 years. In 1967 only 4 colonies, totalling less than 200 nests, were known (Vermeer, 1969). In 1978 the known population had increased to 18 colonies with over 1900 nests. The 1980 population of 2309 nests on 27 colonies is more than a 12-fold increase over the 1967 breeding population (Brechtel, 1981).


120°
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Hay R.
Slave R.
Peace R.
L. Claire
L. Athabasca
Chinchaga R.
Wabasca R.
N
PEACE RIVER
Peace R.
Lesser Slave L.
Cold L.
Smoky R.
Athabasca R.
EDMONTON
Alberta
CANADA
Battle R.
N. Saskatchewan R.
Red Deer R.
Bow R.
CALGARY
Oldman R.
S. Sask. R.
St. Mary R.
49°
DOUBLE-CRESTED CORMORANT COLONIES
Previously active colonies: ○
Presently active colonies: ● 1-99
● 100-300
● over 300
Scale: 0 100 200 300
kilometers

Figure 1 – Presently and previously active Double-crested Cormorant colonies in Alberta, 1980. (Brechtel, 1981).

Previous Research

The Atlantic coast population of the Double-crested Cormorant has been well described. Major ecological studies were carried out more than 50 years ago by Lewis (1929) and Mendall (1936). More recently, Ross (1973) and Hogan (1979) have carried out comparative ecological studies on the Double-crested Cormorant and the Great Cormorant (*Phalacrocorax carbo*), in Nova Scotia and Prince Edward Island respectively.

A variety of studies have also been conducted in the last 25 years on the west coast subspecies (*P. a. albociliatus*) at Mandarte Island, British Columbia. Van Tets (1959, 1965) described basic reproductive parameters and compared reproductive behaviors among the three species of cormorants present on the west coast (Double-crested, Pelagic (*P. pelagicus*), and Brant's Cormorant (*P. penicillatus*)). Robertson (1971) continued the examination of this population by studying feeding and supranormal broods. Van de Veen (1973) expanded on Robertson's & Van Tets' work by describing the demography of the west coast Double-crested Cormorant. As the British Columbia population is essentially non-migratory, comparisons between it and the Alberta population must be done with caution.

In contrast to the east and west coast populations, mid-continent cormorants have not been well studied. Mitchell (1977) published the first extensive account of inland nesting Double-crested Cormorants after studying two arboreal colonies in Utah. Aspects of Double-crested Cormorant habitat selection and reproductive biology related to population control attempts in Manitoba were described by McLeod & Bondar (1953). With few exceptions, publications referring to inland nesting cormorants focus on describing local or regional population status.

In western Canada, Vermeer (1969a, 1969b, 1969c, 1970a, 1970b, 1970c, 1973) documented the population status and commented on aspects of colony initiation and habitat selection by cormorants in Alberta, Saskatchewan and Manitoba. Roney (1977, 1978, 1980) provided information on cormorant status and trend, and published a preliminary examination of the food habits of this species in Saskatchewan. In Alberta, Weseloh et al. (1975, 1977) Markham and Brechtel (1978), and Brechtel (1981) have reported on the recent status of Double-crested Cormorants.

The population status and trend of the entire Canadian population of Double-crested Cormorants has been summarized in a report to the Committee on the Status of Endangered Wildlife in Canada Markham (1978).

II. Study Area

Six Double-crested Cormorant colonies within a 70 kilometer radius of Brooks, Alberta (50.6°N x 111.9°W) were studied between April and September of 1978, 1979 and 1980 (Figure 2). All of these colonies were located on islands in artificial waterbodies created for irrigation or waterfowl production purposes. Waterlevels in each waterbody are regulated annually, normally being drawn down in spring and early summer for irrigation purposes and refilled in fall and spring with water diverted from the Bow River. Barkhausen Lake, however relies on local runoff and is not used for irrigation.

The region is dominated by mixed prairie vegetation (Copeland 1950) and includes the area previously described by Keith (1961). A brief description of each colony island is provided below.

Lake Newell

The Newell colony is located on Pelican Island in the southwest corner of Lake Newell, approximately 19 kilometers southwest of Brooks Alberta. It is the largest colony in Alberta and contained over 33% of the provincial breeding population in 1980. The colony was established at least 35 years ago (Randall 1946) and is the oldest in the study area. A 1927 report by Munroe suggests that the island was originally colonized by either California (*Larus californicus*) or Ring-billed (*L. delawarensis*) Gulls.

The reservoir was created in 1912-14, first flooded in 1915 and approached present levels in the mid-1930's. Water is provided from the Bow River via a canal from the Bassano Dam. The bed of Lake Newell, its islands and surrounding uplands are owned by the Eastern Irrigation District (E.I.D.), a user-owned co-operative of irrigation farmers. At normal water levels, Pelican Island is a rough oval of approximately 50 x 100 m. The island has a gently undulating surface which is between 1.5 and 2.5 m above water, depending on reservoir levels.

Water erosion had decreased the size of the island over many years to a minimum during 1978. Increased reservoir levels in 1977 and 1978 were then threatening the continued existence of the island. The Alberta Fish and Wildlife Division, stabilized the island at its present size by adding soil to the central portion and protected the steep outer slopes with rip rap (rock & boulders) to prevent further erosion (Anderson 1982).

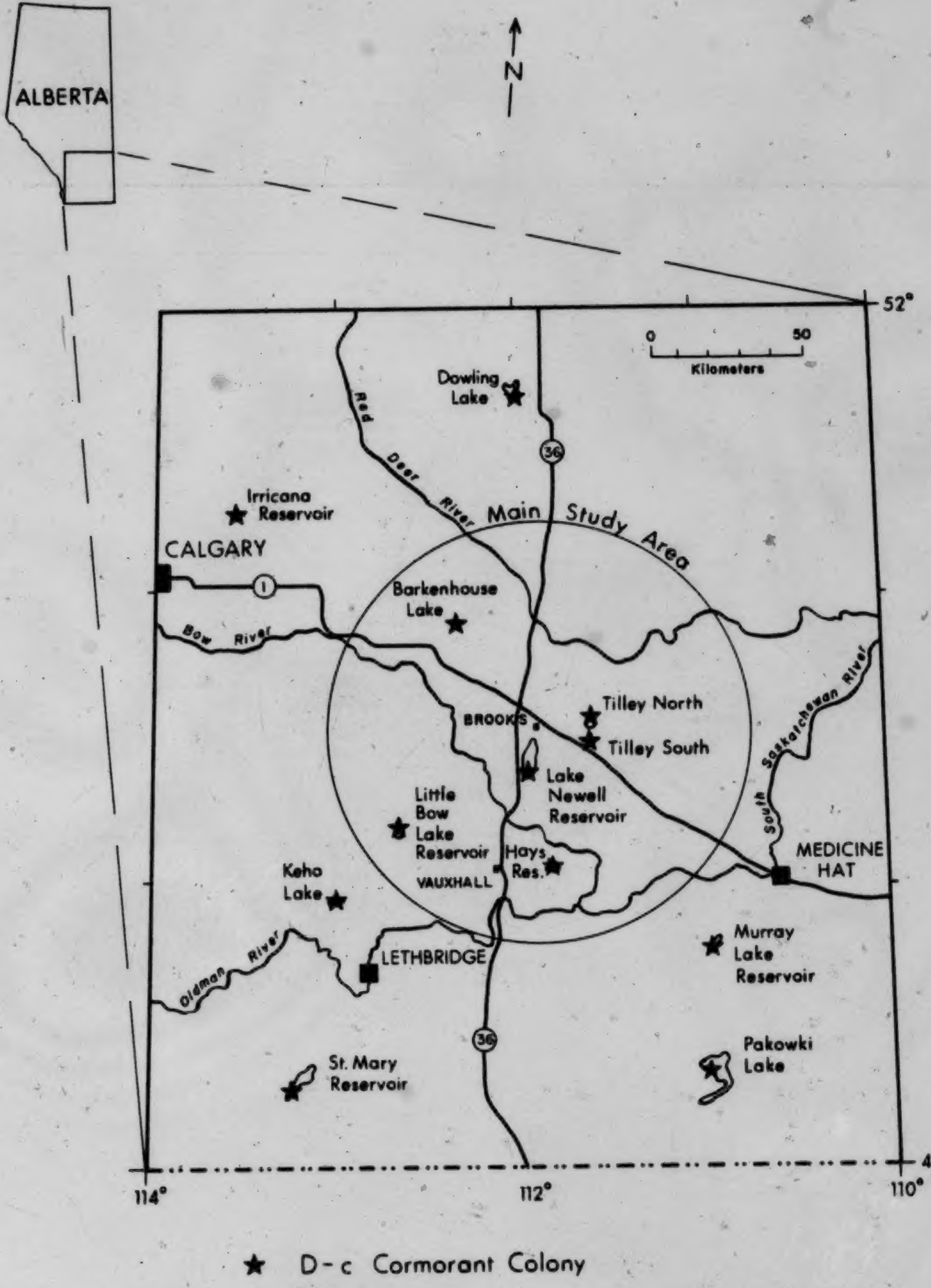

ALBERTA
N
52°
0
50
Kilometers
Dowling Lake
Red Deer River
36
Irricana Reservoir
Main Study Area
CALGARY
1
Barkenhouse Lake
Bow River
Tilley North
BROOKS
Tilley South
South Saskatchewan River
Lake Newell Reservoir
Little Bow Lake Reservoir
Hays Res.
MEDICINE HAT
Keho Lake
VAUXHALL
Murray Lake Reservoir
Oldman River
LETHBRIDGE
36
Pakowki Lake
St. Mary Reservoir
49°
114°
112°
110°
★ D-c Cormorant Colony

Figure 2 – Location of study area and active Double-crested Cormorant colonies in southern Alberta, 1978–1980.

The vegetation on the island is not typical of the short grass prairie from which it originated. At present, vegetation covers from 40 to 50% of the island. The remaining areas are kept open by the activities of nesting cormorants. The vegetation which does survive is comprised, almost exclusively, of broad leaved annuals and perrenials, dominated by false ragweed (*Iva xanthifolia*), burning bush (*Kochia scoparia*), lambs quarters (*Chenopodium album*) and tansy mustard (*Descurainia sophia*).

There is a distinct annual cycle of association between the cormorants and this vegetation. In the spring, cormorants return prior to the initiation of plant growth and utilize virtually all of the previous years dead plant stalks for nesting material. Germination and survival of plants under or near nesting and loafing areas is prevented, probably due to physical and chemical effects of the nesting cormorants. As summer progresses, the vegetation grows in unoccupied areas and may surround groups of nests with a visually solid wall from 0.5 to 0.75 meters high. On the Newell colony, nesting density is high enough that vegetation is eliminated from a large portion of the island and most nesting birds have an unobstructed view of the water.

Between 1978 and 1980 cormorants attempted to nest on three other islands in Lake Newell, and in 1980 at least six young were fledged from a small island approximately 1.7 km southeast of Pelican Island. These nesting attempts are not included in the Newell colony data.

Tilley North

The Tilley North colony was located on a small (40 x 85 m) island created by Ducks Unlimited prior to the flooding of the Tilley 'B' reservoir. This irrigation reservoir is located approximately 16 km northeast of Brooks, Alberta and was created in 1973-74. The island was a relatively smooth hummock rising approximately 2 m above water level from a broad shoreline, and located approximately 300 m from the closest mainland shore in 1978.

Vegetation cover on this island was composed of a lower-growing grass-forb mixture including burning bush, tansy mustard, lambs quarters, foxtail barley (*Hordeum jubatum*), western wheat grass (*Agropyron smithii*) and crested wheat grass (*A. cristatum*). The area of vegetation suppressed by cormorant activity ranged from 4 to 5% of the island. Cormorants began nesting on this island only one or two years after it was created (first documented nesting in 1976). The E.I.D. began to increase the water levels in this reservoir in 1979 and by 1981 the colony island was totally submerged.

Tilley South

This colony is located on a broad low island (80 x 112 m) in the southwest corner of the Tilley 'A' reservoir, 9 km South of the Tilley North colony. The island was formed when this Ducks Unlimited waterfowl reservoir was flooded in 1973. It is owned by the E.I.D. and located approximately 300 m from the closest mainland shore. It is a very low-lying island and may change in size by 50% or more depending on water levels. The island's vegetation reflects this, with much of the shoreline being covered with emergent type vegetation such as spike rush (*Eleocharis palustrius*) and water smartweed (*Polygonum coccineum*). The upland portion of the island is similar to the Tilley North colony with the addition of limited stands of bull thistle (*Cirsium vulgare*) and false ragweed.

Cormorants first nested on this island in 1977, four years after it was created. In addition, both California and Ring-billed Gulls have nested here since at least 1976. In 1980, a complete census of the island revealed 422 California and 889 Ring-billed Gull nests.

Hays

The Hays colony is located on a small island in Hays (also known as Scope) Reservoir, 17 km east of Vauxhall, Alberta. This island, depending on the highly variable water levels in this shallow reservoir, is either separate from or connected to a larger complex of islands on the north side of the reservoir. This is the only island in the study area which is frequently connected to the mainland by mudflats during late summer minimum water levels.

The reservoir was created in 1954 by the Bow River Irrigation District who own the island and surrounding shoreline. Cormorants colonized this location between 1967 and 1971. A large colony of both California and Ring-billed Gulls was established on these islands prior to 1967 and is still active.

In 1980, the gull nesting groups adjacent to the cormorant colony consisted of approximately 100 California Gull nests and 2100 Ring-billed Gull nests. The total gull population on this and adjacent islands is several times this number.

The vegetative composition of this island depends greatly on the fluctuation in water levels. The dry upland areas are dominated by tall forbs such as burning bush and lambs quarters. The lower areas which are flooded for a portion of the year exhibit a more aquatic vegetation including cocklebur (*Xanthium ilalicum*), spike rush and smartweed.

Smaller cormorant colonies were established in 1979(2) and 1980(1) on the high points of the adjacent or connected island complex. These, however, were relatively unsuccessful and are not included in the reproductive data analysis.

Little Bow

The Little Bow colony is located on a small (23 x 67 m) island in the northwest arm of Little Bow Reservoir, 55 km north of Lethbridge, Alberta. The island and surrounding area are owned by the Lethbridge Northern Irrigation District. The reservoir was flooded in 1920 for irrigation purposes but cormorants were not observed to nest here until 1965 (Brechtel 1981). Once again, California Gulls preceded cormorants as colony occupants and 221 pairs nested there in 1980.

The island on which this colony was located between 1965 and 1976 was lost to erosion in 1976-77. Both gulls and cormorants successfully relocated to the nearest adjacent island in 1977 and continued to use this site in subsequent years.

The vegetation on this island is similar to other nesting sites and is dominated by burning bush, lambs quarters and false ragweed.

Barkhausen

The Barkhausen colony is located on a natural island in Lake Barkhausen, 11 km northeast of Bassano, Alberta. This waterfowl production reservoir was created in 1945 by Ducks Unlimited. The colony island is roughly circular with a diameter of approximately 15 m and a vertical height of no more than 1 m above water level. This is the smallest nesting site used by cormorants in Alberta. Even so, California Gulls nested on this island prior to and after the 1977 colonization by cormorants.

The vegetation on this colony is unique in southern Alberta in that roughly 40-50% of the island is covered by low (2-4 m) willows (*Salix* spp.). In addition, burning bush and lambs quarters grow on unoccupied areas to a height of 0.5-1.5 m.

III. Methods

A variety of data collection techniques were employed to document various aspects of Double-crested Cormorant reproductive ecology. The majority of these techniques fall into two broad categories: off-colony or on-colony observations. A colony is defined as a geographic locality at which cormorants nest. Colonies are often subdivided into smaller groups of adjacent nests referred to as subcolonies.

A. Off-Colony Observations

During 1978, and to a lesser extent in 1979 and 1980, all colonies were observed from a distance. Each spring, colony initiation dates were documented by frequent (normally twice-weekly) observation of each colony until the first cormorants arrived. In May of 1978 observation blinds were constructed on islands adjacent to the Newell and Tilley North colonies at a distance of 250 m and 270 m respectively. During each year, daily (1978) and at least twice-weekly (1979 & 1980) observations were conducted from these blinds. Observation times were varied to include all periods from dawn to dusk.

During each observation period a variety of data was collected using a 20-45x spotting scope. A complete census of adults and subadults on and off nests was made using the lighter subadult plumage as the distinguishing criterion. Double-crested Cormorants typically do not acquire complete adult plumage until 3 years of age. As the young of the year grow larger and attain full juvenile plumage and adult feathers lose their sheen and become progressively more brownish, the distinction between adult and subadult becomes increasingly difficult and is unreliable by mid-July. Palmer (1962) indicates that plumage is not a safe age criteria in Double-crested Cormorants as some two year olds will appear younger than some yearlings, and some apparently adult birds are, in fact, two year olds. It is, however, safe to identify light plumaged birds as yearlings or two year olds. All dark birds, however, cannot be positively identified as adult and the subadult census is therefore a minimum estimate.

During 1979 and 1980 observations of color banded cormorants allowed calculations of return rate. They also allowed documentation of 'subadult' reproductive activity and success. Limited behavioral observations were also collected from blinds which allowed the identification of various reproductive stages, particularly courtship and nest occupancy. Data on nest specific reproductive behavior and success (1978) were collected after a sample of nests were individually marked with numbered stakes visible from the blinds. General observations on inter- and intraspecific interactions, subcolony establishment, colony occupancy, and fall departure were also collected from blinds.

Less detailed and less frequent observations at the Hays, Tilley South, Barkhausen and Little Bow colonies were collected from shoreline observation areas approximately 500 m, 350 m, 230 m and 500 m from the colony sites respectively. The quality of these observations decreased as vegetation adjacent to the colony grew and prevented a clear view.

An aerial survey of waterbodies in southern Alberta was carried out in late May or early June in each year of the study. In addition to observing all active cormorant colonies I examined a large number of potential nest sites and waterbodies for colonial nesting birds. It was during these surveys that the newly established colonies at Keho Lake and Pakowki Lake were first discovered.

B. On-Colony Observations

In all years, each colony was visited at least once per month, normally during the first week of May, June and July. Comprehensive information on the number of active and inactive nests, and the numbers of eggs and young in and out of nests was collected. In addition, the vegetation pattern, size and shape of the island, colony and subcolony location and the height class, location, and contents of all nests were documented at least once per year on each island. Nests were divided into three height classes: low = 0-15 cm, medium = 16-30 cm, or high > 30 cm. Absolute height, nest diameter and distance to nearest adjacent nest were also recorded for all individually marked nests. A census of active gull nests on each colony island was carried out in late May 1980.

During 1979 and 1980 several colonies were visited weekly (Newell 1979 and 1980, Hays 1980) or twice-weekly (Tilley North 1979 and Tilley South 1980). Detailed nest specific data were collected from all nests on Tilley North and South and from a sample of the Newell (14%) and Hays (21%) colonies.

In all of these colonies each egg in a staked nest was individually marked to identify the date laid and laying sequence. In cases where more than one egg was laid between observation periods, laying sequence was estimated by the relative amount of nest staining on each egg. This allowed the computation of nest, subcolony and colony specific reproductive output (e.g., clutch size) and the calculation of reproductive success parameters (e.g., hatching success). The following parameters were documented:

A nest site may be occupied by a male several days or weeks prior to pair formation and copulation (Mendall 1936, Mitchell 1977). It was, however, not possible to determine if the same individual or pair occupied the nest until eggs were laid. The most accurate measure of when a breeding pair formed and began a nesting attempt was, therefore, the day on which the first egg was observed. Although one or both of a pair may have occupied the nest prior to this, the resulting 'nest initiation date' provided a definitive and broadly comparable point for analysis of the timing of reproductive events.

As a measure of overall female reproductive effort, the sum of all eggs laid during one nesting period was recorded and defined as 'total laid'. A nesting period required continuous occupancy and was terminated when all eggs or young disappeared from a nest and no new eggs were laid within 10 days. The reuse and laying of eggs in a previously occupied nest more than 10 days after the termination of laying by the original occupants was defined as a renest. Renests, therefore, may include occupancy by the same male, female or pair or use by a different male, female or pair. No sure way to identify individuals was found and renests are therefore treated separately from the main body of data relating to first nests.

'Clutch size' was defined as the maximum number of eggs observed in a nest during a single observation in the nesting period (Thompson 1964, Mitchell 1977). In virtually all cases (496 of 497 nests), this figure also represents the number of eggs in a nest at the termination of laying (Robertson 1971). In many cases, a female cormorant will continue to lay eggs well beyond the normal clutch size if eggs are removed prior to clutch completion. This suggests that Double-crested Cormorants are at least partially indeterminate nesters and the maximum instantaneous clutch count is therefore the most appropriate clutch size measure (see Results: clutch size).

'Pre-clutch success' is an indicator of egg loss prior to clutch completion, calculated by dividing clutch size by 'total laid'. Both of these measures assume that only one female laid in each nest and that no eggs were lost prior to being marked for the first time.

'Incubation period' was defined as the total number of days an egg is present in the nest prior to hatching. There is not aggreement on when functional incubation (the application of heat by the female cormorant) begins in Double-crested Cormorants. Drent et al. (1964) and Mitchell (1977) suggest that incubation begins with the first egg while Lewis 1929 and Palmer 1962 report it beginning with later eggs in a clutch. The measure I used may, therefore, slightly overestimate the effective incubation period. Any egg which stayed in the nest for more than 35 days was assumed to be either infertile or addled.

'Brood size' was defined as the maximum number of small young after hatching and prior to the young being able to leave the nest. Hatching success is calculated either on a nest specific basis (brood : clutch size) or by documenting the fate of individual eggs by category (i.e., size, position in laying sequence). The former has the advantage of being a figure comparable to later estimates of fledging and nesting success. The latter provides the potential for a more detailed examination of factors responsible for differences in hatching success. It was assumed that if an egg was lost between the observation periods when it should have hatched, that it was lost as an egg and did not contribute to brood size or hatching success. These measures are therefore conservative estimates.

As only a small number of young were individually marked, it was not generally possible to document the fates of individual chicks after hatching. Similarly, nest specific data are only reliable until young reach approximately three weeks of age. At 3 weeks young can and do leave their nests in response to the presence of an observer on the colony. Fledging success was, therefore, defined as survival until 18 days of age. By this age young are able to thermoregulate (Dunn 1976) and are not normally subject to gull predation (Mendall 1936, Robertson 1971). Van de Veen (1973) found that "... all natural mortality happened within three weeks after hatching, ...".

The age of individual young and their survival to fledging were documented in two ways. First, unless otherwise indicated by other observations, young were assumed to disappear in the inverse order of hatching. Thus, the first young to disappear would be assumed to be the youngest and would not be assumed to have fledged unless it and all it's siblings were at least 18 days old. The second factor used to determine survival to fledging (18+ days) was the eruption of primaries from their sheaths. Several previous authors have documented feather development, indicating that primaries emerge between 16 and 19 days of age (Lewis 1929, Mendall 1936, Mitchell 1977). In order to be included as a fledgling, an individual had to fulfill both of these criteria. 'Nesting Success' was calculated by dividing the number of young fledged in a nest by the original clutch size of that nest.

'Post banding survival' was the final estimate of on-colony reproductive success and was calculated by dividing the number of dead banded young found on a particular colony by the total number of young banded on that colony that year. This percentage is applicable only at the colony level and is a minimum estimate as some banded young which died on-colony may not have been found.

The accuracy of these reproductive parameters is dependent on the frequency of observation. By visiting colonies only once or twice a week, disturbance is minimized but data quality suffers. It is, however, assumed that by consistently ascribing the laying, hatching and nestling dates to the midpoint between observation dates, and by providing a large sample size, variations in these data will average out and that they do provide an accurate estimate of actual reproductive performance.

C. Disturbance

Colony, and in some cases subcolony, reaction to disturbance was recorded during and after each visit to a nesting island. A small (4 to 6m) boat with an outboard motor was used to reach the islands. Observations included relative speed, and direction of approach, distance at which the first and then 100% of the cormorants left the island (flush distance), duration of disturbance, the time it took for the first cormorant to return to the colony (first return), and the time it took for all of the active nests to be occupied (100% return). In addition, notes were kept on gull predation and the location and behavior of the displaced cormorants. Similar data were collected whenever a non-research human disturbance occurred during an observation period in a blind.

Reproductive and egg mortality data were compared between intensively (twice weekly), moderately (once weekly), and slightly (once per month) disturbed colonies. Intensively and moderately disturbed colonies were compared using detailed nest-specific data and success parameters. In order to compare equivalent data between these and slightly disturbed colonies, however, it was necessary to use the less precise measures resulting from single colony visits at the beginning of May, June and July. On small colonies it was possible to estimate overall reproductive success by dividing the total number of late season young by the number of active nests and adding a correction factor for unhatched eggs (number of eggs x 0.42378, the mean nesting success for all individually studied eggs). This estimate was calculated using data from mid-July. Active nests in this instance are defined as those which appear to have been used in the present year. Inactive nests have a distinctive appearance. Nest material in unused nests is taken by adjacent breeding birds and unused nest structures therefore disappear or are reduced to low rounded mounds. This, however, is a minimum estimate, as some nests which had been previously active but failed early in the season would be omitted.

This type of estimate was often not calculated on larger colonies (Hays, Newell) as it was usually not possible to accurately census the large number of highly mobile young found on these colonies. Subcolonies within these colonies were also highly asynchronous. There were, therefore, young old enough to swim away from the colony prior to the final completion of laying.

D. Marking of Young

During 1979 a number of young were patagium tagged with numbered chick wing bands (Monel, no. 3) shortly after hatching to allow a later analysis of survival within broods. Tagging always occurred within the first 7-13 days of life. When two or more young in a nest were tagged on the same day, size differences were used to estimate hatching sequence. Although this allows some room for error, cormorants hatch asynchronously, and the smallest chick in a nest is normally the youngest. Growth rates were calculated in 1980 by weighing marked young twice weekly until they were 4-6 weeks old with 500 g, 1000 g, or 5000 g 'Pezola' spring balances.

During all years of the study, nestling cormorants more than three or four weeks of age were banded on the left leg with numbered aluminum leg bands provided by the United States Fish and Wildlife Service through the Canadian Wildlife Service. In addition, at the Newell, Hays, Tilley North and Little Bow colonies, colored plastic leg bands were attached above the aluminum band to identify the colony on which the individual was hatched (yellow, white, orange and red respectively). Yellow, red or orange bands were also placed on the right leg to identify the year in which the young cormorant was hatched (1978, 1979 or 1980 respectively). In 1979 and 1980 a colored year band was placed on the right leg of birds banded at all colonies. The only exception to this sequence is that birds hatched at the Newell colony in 1978, were marked only by an aluminum band on the left leg and a yellow band on the right. A total of 3606 nestling cormorants were banded with aluminum bands between 1978 and 1980. The natal colony and year of hatching of 2869 of these were identified with colored plastic leg bands. The age class of an additional 604 of the banded young was identified by a single color band on the right leg only.

In all, approximately 65% of the cormorants fledged in southern Alberta between 1978 and 1980 were banded with aluminum bands and 64% of the young fledged from the Newell, Hays, Tilley North and Little Bow colonies in this same period were color banded.

Colored and numbered plastic patagial tags were applied to a small sample of young from the Newell (12 in 1978, 38 in 1979) Hays (50 in 1979) and Tilley North (50 in 1979) colonies. Tag colors were the same as leg band colony identification colors (yellow, white and red respectively), and each tag bore a black number from 1 to 50.

A portion (76%) of the plastic patagial tagged young from Tilley North in 1979 had been previously tagged with numbered Monel patagial tags at hatching. As each active nest was individually staked and numbered at Tilley North in 1979, it was possible to identify the nests at which many of these individually marked fledglings were hatched. Unfortunately, as the Tilley North colony island has subsequently been destroyed these data are less valuable than they might have been.

E. Other Techniques

Several ancillary techniques were employed to explore specific aspects of Double-crested Cormorant biology. Egg size and weight were determined by measurements of both marked eggs in nests and eggs which had been collected after rolling or being kicked out of a nest. Throughout the study an effort was made to recover marked eggs, and to a lesser extent unmarked eggs, from nest bases. Length and maximum width were measured with a dial caliper accurate to 0.01 mm, and weight was measured with either a spring or triple-beam balance.

A sample of seven dead young between three and six weeks of age was collected following a large scale mortality on the Hays colony in late June 1980. These were submitted to the Animal Health Division Laboratory of Alberta Agriculture for post mortem examination and determination of cause of death.

In order to compare reproductive parameters between intensively studied colony types, colonies were divided into two general categories. Data from the Tilley north 1979 and Tilley south 1980 colonies were pooled in a 'new small' category. Both of these were 4 years old and contained 62 and 127 active nests respectively in the years studied. Data on 'old large' colonies were collected at the Newell 1979 and 1980 and Hays 1980 colonies. The Hays colony was established at least 9 years prior to 1980 and contained 329 active nests when studied. The Newell colony was established prior to 1945 and is the oldest known cormorant breeding site in southern Alberta. It is also the largest colony in the province, with more than 700 active nests in both 1979 and 1980.

F. Analytical Technniques

The majority of the statistical analyses applied to the reproductive success and reproductive output parameters relied on non-parameteric rank order or frequency tests of significance. The truncated, non-normal distribution of these data combined with the wide ranges in variance precluded the application of parametic tests.

The data were stored, organized and statistically tested using the Michigan Interactive Data Analysis System (MIDAS, Fox and Guire 1976) available through the University of Alberta Computing Services Centre. The Mann-Whitney U-statistic test (MW'U') was used to compare reproductive output parameters (clutch size, brood size, etc.), nest initiation dates and nest site characteristics (height, nearest neighbour). Reproductive success measures were compared using Chi-squared tests (Chi²). If observed sample size in a contingency table comparison were less than 5, a Fishers Exact Test was used. Rank order correlations were carried out using the Spearman's rank order correlation coefficients (Rho).

In order to facilitate numerical and statistical calculations with calendar dates each day was given a sequential number, from 1 for January 1 to 365 for December 31. These numbers were normally converted back to the more familiar calendar dates for discussion.

IV. RESULTS

A. Annual Cycle in Alberta

The following section describes the annual reproductive cycle of Double-crested Cormorants in Alberta during the summers of 1978 to 1980. Data and descriptions of activities are divided into 15 generally sequential categories. Detailed reproductive data are mostly from the 1979 and 1980 seasons, while descriptions and comparisons are made from observations collected in 1978, 1979 and 1980. A visual summary of reproductive events in first and renests is provided in Figure 3.

Spring Arrival

In all years the first cormorants were observed on southern Alberta colonies between April 18 and 20. First arrival dates appeared to be independent of the ice conditions as colony lakes varied from being 75% ice covered two weeks after arrival to being completely ice free prior to first return. Vermeer (1970a) reported a similarly consistent arrival date (April 16) and variable ice free dates (April 2 - 21) in 1968 and 1969 at Lake Newell. Cormorants were always observed earlier on the older, larger colonies (Hays, Newell) than at the more recently established smaller locations (Tilley North, Tilley South and Barkhausen).

Daily mean temperatures taken at Brooks Horticultural Station during late March to late May 1979 and 1980 are shown in Figure 4. April and May of 1979 were cooler by 1.8°C than the long term average at Brooks and the equivalent period in 1980 was 3.4°C warmer. Mean temperature between first arrival and mean nest initiation date was 4.9°C in 1979 and 13.3° in 1980.

Partially due to this difference in temperature, Lake Newell became ice free earlier in 1980 (April 20) than in 1979 (May 3). Although cormorants were first observed on April 18 in both years, the number of adults on-colony increased much faster in 1980 (May 5 census: 1979 = 478, 1980 = 820 adult cormorants).

Yearling and two year old cormorants always returned to the breeding islands later than adults. Observations at the Newell and Tilley North colonies in 1979 and 1980 showed that the first yearlings arrived, on average, 23 days later and two year olds arrived 12 days later than the first adults. Color-marked yearling cormorants were first

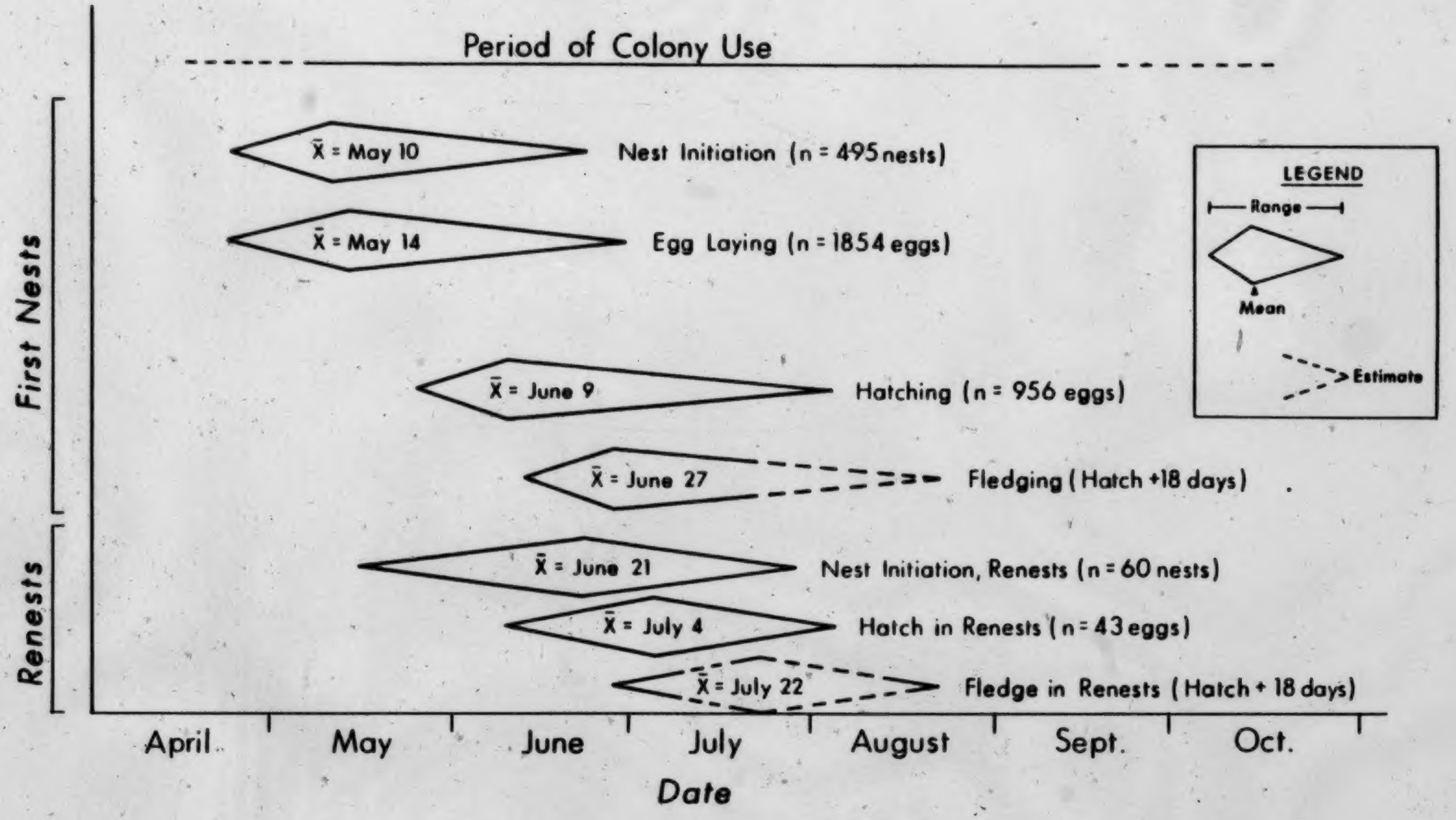


Figure 3 - Chronology of reproductive events for Double-crested Cormorants in southern Alberta, 1979 and 1980.

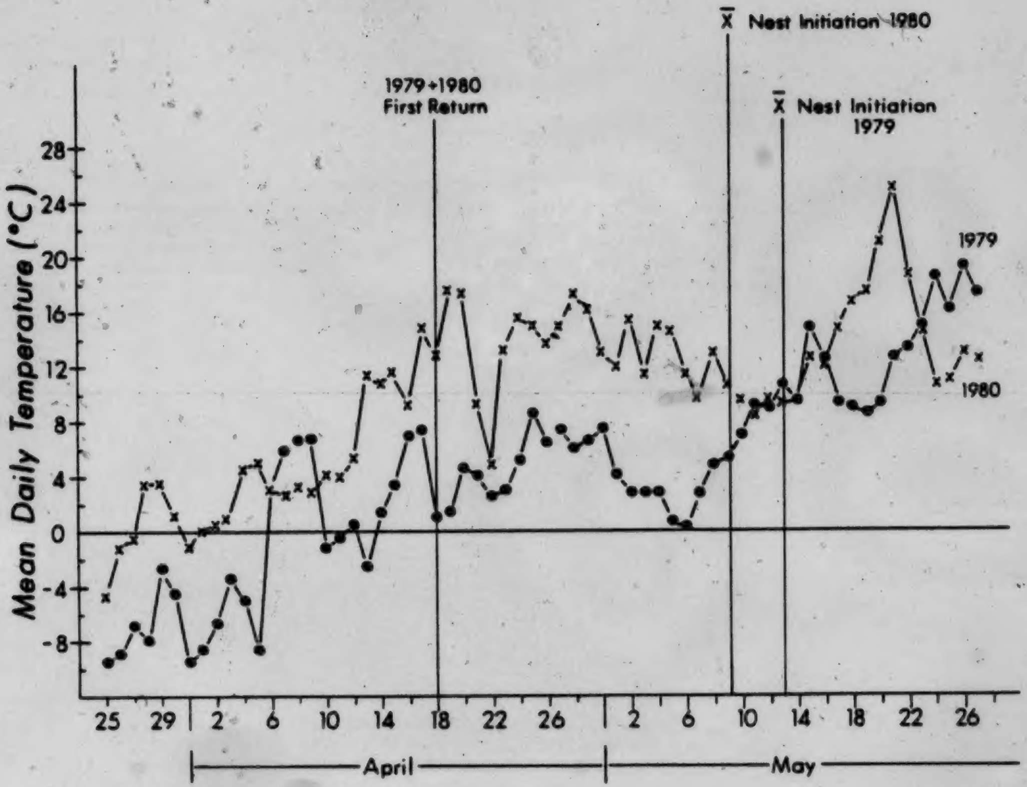


Figure 4 – Daily mean temperature at the Brooks Horticultural Station, 1979 and 1980.

observed 2 days earlier at Lake Newell, and 14 days earlier at Tilley North in 1980 than in 1979. Annual weather variation did not appear to influence the earliest spring migrants, but may have influenced the rate of return of both subadult and adult cormorants.

Although the sexes are externally monomorphic, they could be segregated during courtship by unique behavioral displays. The male-specific wing-flip display described by Van Tets (1965), was used to determine that a large proportion of the early migrants were male. For example, on April 29, 1979, of 18 adults on or near the Tilley North colony site, 6 (33%) were members of mated pairs, 10 (56%) were actively courting males, one was an unmated female, and one was of unknown sex. A similarly unbalanced sex ratio was also observed during the early establishment of subcolonies at both the Tilley North and Newell colonies. It would appear that male cormorants may have returned to the nesting islands slightly earlier than females, and that it was males who initially colonized new subcolonies.

Courtship

Double-crested Cormorant reproductive behavior has been described by several authors (Van Tets 1959, 1965; Mendall 1936; Lewis 1929). In southern Alberta, the male chose a nest site, normally a previously used nest structure, and attracted a female to the nest using a stereotyped wing-flip display (Van Tets 1965). A territory was comprised of a nest site and a small radius (approximately one head and neck length) around it. The mean internest distance (center to center) for 456 nests was 72.5 cm.

Prior to pair formation, territories were defended against other males and after pair formation, against all other cormorants. Gulls and magpies (*Pica pica*) were also excluded from the immediate vicinity of the nest, but were allowed to scavenge in open areas of the colony island. Occasionally, competition for previously used nest sites resulted in the displacement of a courting male prior to pair formation but generally nests appeared to be re-occupied on a first-come first-served basis.

Once a pair had occupied a nest, the site was not normally left unattended until the young had attained two or three weeks of age, or the nesting attempt had failed. Early in the season nest material was often stolen from unattended nests. If abandoned, nests often disappeared entirely due to the theft of nesting material by other cormorants. This is a factor which must be considered when estimating the breeding population by nest counts made late in the season.

Copulation was observed only on the nest, and is usually followed by the male offering a piece of nesting material to the female.

Nest Initiation

The overall mean nest initiation date was May 10. Dates ranged from April 23 to June 22, with 95% of all nests being initiated by May 27. The sequence of nest initiation dates on study area colonies is shown in Figure 5.

Although the majority of nests were begun between the last week in April and the third week in May, new nests were initiated until the third week of June. This pattern suggests that birds returning late are not necessarily excluded from breeding.

All nests initiated later than May 31 were on the older, larger colonies (Newell, Hays, n = 14). It should be remembered that these calculations exclude renesting attempts occurring in the same nest, but may include individuals or pairs which had failed earlier and nested again at a new site. Although renesting will be discussed later, it is interesting to note that while old, large colonies comprised 62% of the nest sample, they contained 90% of the renesting attempts. It appears that birds nesting on larger, older colonies are more likely to renest than those nesting on newer, smaller colonies.

The pattern of mean nest initiation dates of different colonies was similar to the pattern of first arrivals, being earlier at the older, larger colonies than the smaller, younger colonies (old: mean initiation date = May 9, young: mean = May 13, MW'U' $p < .0001$). This relationship was consistent and significant both within and between years (MW'U' 1979 $p < .0001$; 1980 $p < .0001$). Annual variation also followed the previously mentioned pattern with nests being initiated earlier in the warmer spring of 1980 than the cooler spring of 1979 (1979 mean initiation date = May 13, 1980 mean = May 9; MW'U' $p < .0001$).

Spatial Variation

When cormorants return to a previously used colony they are confronted with a variety of possible nesting sites. The choices which breeding birds make provide insight into habitat selection priorities, and should have implications for later nesting success.

There was a definite pattern to the sequence of nest initiation on a colony island. Subcolonies were occupied sequentially with each being initiated before the previous one

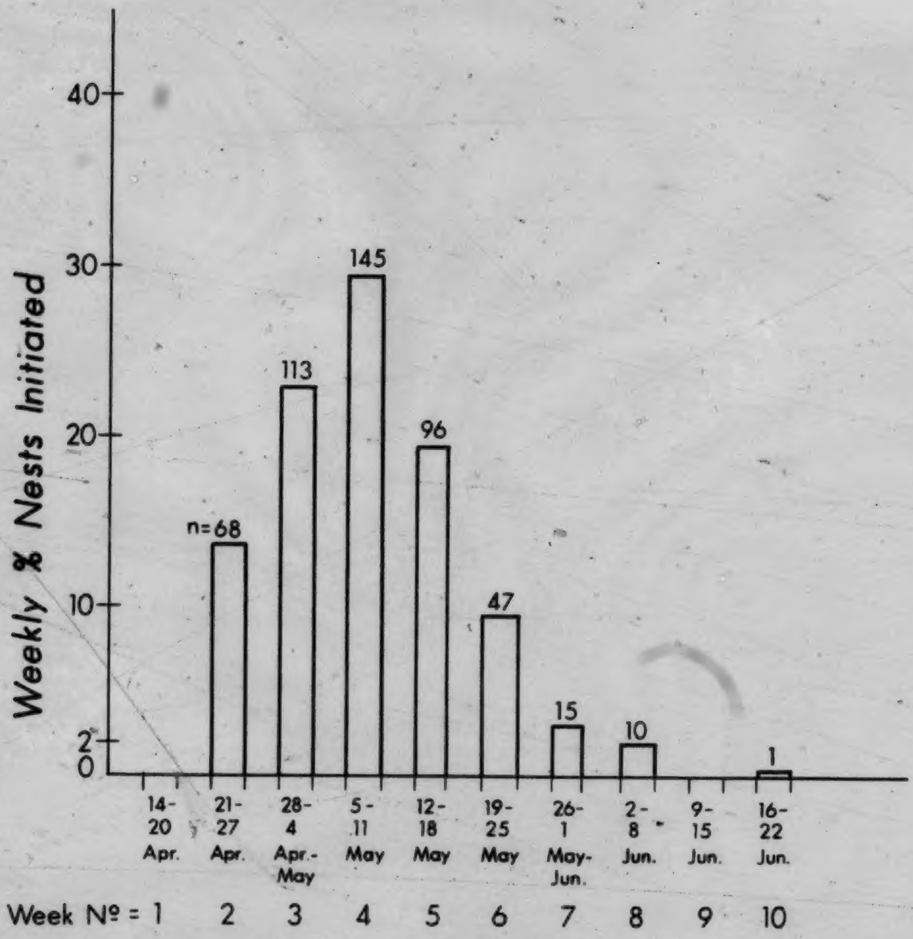


Figure 5 – Distribution of Double-crested Cormorant nest initiation dates by week, 1979 and 1980.

had ceased to expand. The mean initiation dates and locations of subcolonies on the Newell 1979 and 1980 colonies are shown in Figure 6. This pattern was typical of the larger colonies. Smaller colonies had fewer subcolonies but exhibited the same sequential pattern.

The pattern of nest initiation within subcolonies was most clearly documented at the Tilley South colony in 1980 when reused nests were marked before they were occupied, and new nest sites were marked as they were established. The weekly pattern of initiation for both subcolonies active in 1980 is shown in Figure 7.

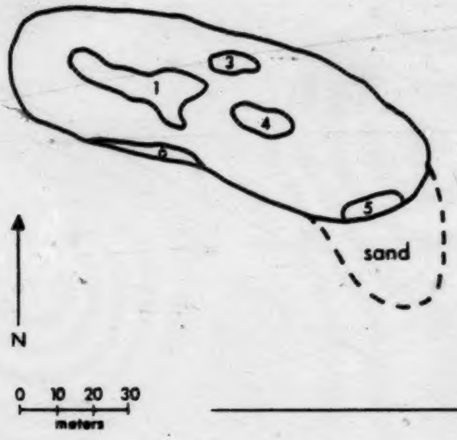
Reproductive Parameters in relation to Initiation Date

In order to examine whether differences in initiation date influenced reproductive output or success I compared nest specific reproductive parameters with nest initiation date (Figure 8, 9). In all parameters examined (total eggs layed, clutch size, brood size and number of young fledged per nest) reproductive output decreased as the season progressed (Rho $p < .0001$ for all parameters). Although the small sample of later nests tended to limit the reliability of late season observations, clutch size and the total number of eggs layed appeared to be more consistent over time than brood or fledgling numbers.

A similar trend is clear in the relationship of nest success parameters to nest initiation date (Figure 9). The relative stability of pre-clutch success reflects the fact that both the total eggs laid and the clutch size decrease at near the same rate over the reproductive season (Figure 8). The rather drastic decline in other success parameters reflects an increasing ratio of eggs laid per young hatched or fledged as the season progresses. This represents a decrease in the ability of nesting birds to hatch or raise young, independent of the number of eggs laid.

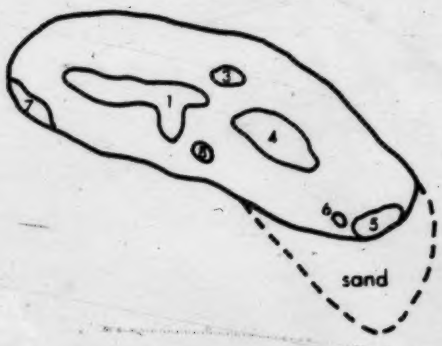
The overall reproductive impact of these data can best be visualized by comparing the number of young fledged per nest with the initiation date of the nest (Figure 8). It is clear that reproductive output declines significantly as the season progresses and if initiation date reflects return date, then cormorants which return earlier have a much greater reproductive output. They not only produced larger clutches but were more successful at hatching their eggs and raising young than breeding birds which returned and/or initiated their nests later in the season.

1979


1
3
4
6
5
sand
N
0 10 20 30
meters

Subcolony Nº	Mean Initiation Date	S.D.	n
1	May 7	5.8	57
3	May 13	7.9	20
4	May 17	5.8	15
5	May 26	6.3	4
6	June 2	2.7	5

1980


1
3
4
7
8
6
5
sand

Subcolony Nº	Mean Initiation Date	S.D.	n
1	May 2	6.6	58
3	May 7	6.9	18
4	May 13	9.7	27
5	May 12	4.5	8
6	May 11	0	4
7	May 20	3.1	9
8	June 13	8.1	3

Figure 6 – Locations and mean nest initiation dates of subcolonies on Pelican Island, Lake Newell, 1979 and 1980.

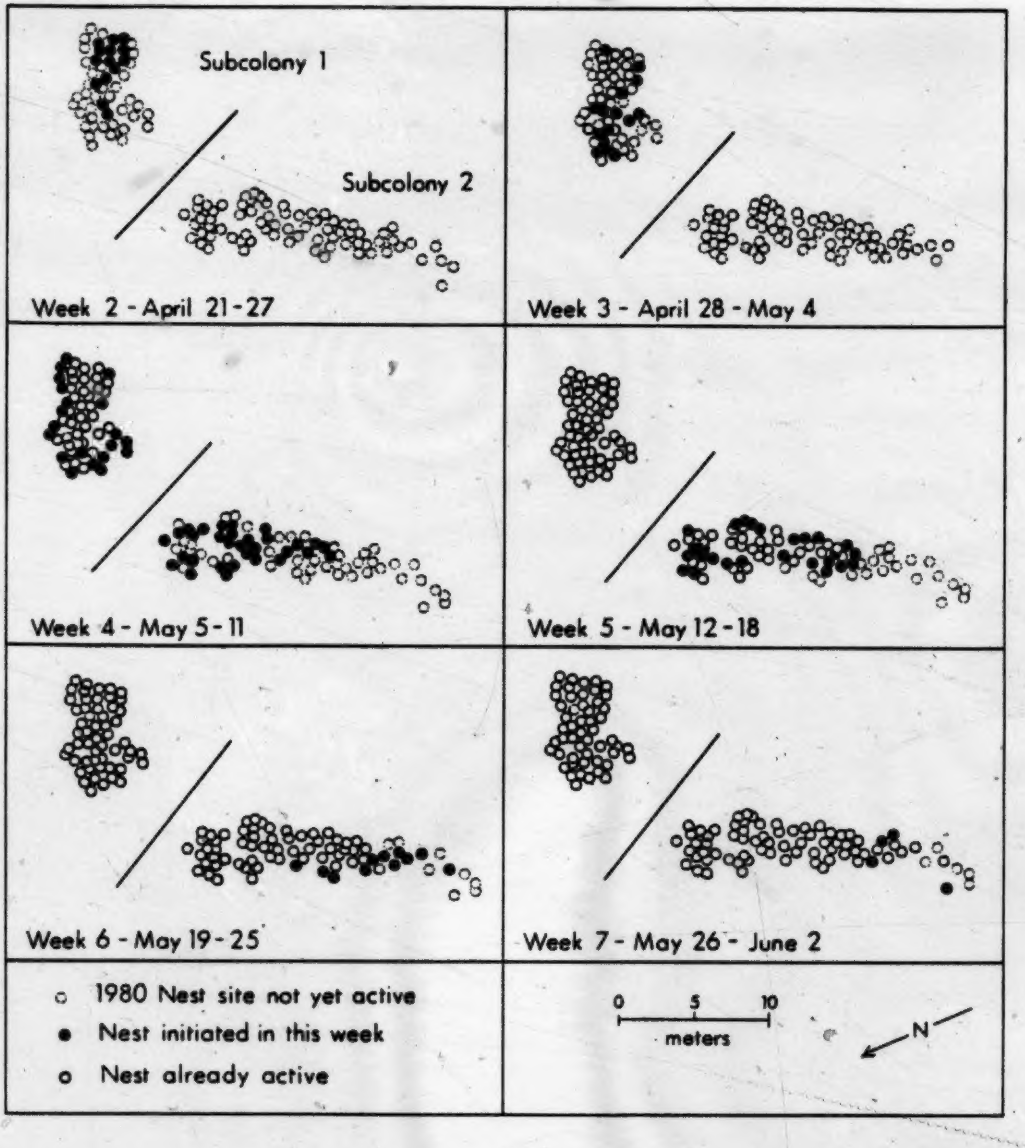

Subcolony 1
Subcolony 2
Week 2 - April 21-27
Week 3 - April 28 - May 4
Week 4 - May 5-11
Week 5 - May 12-18
Week 6 - May 19-25
Week 7 - May 26 - June 2
○ 1980 Nest site not yet active
● Nest initiated in this week
○ Nest already active
0
5
10
meters
N

Figure 7 – Weekly nest initiation pattern at Tilley South in 1980.

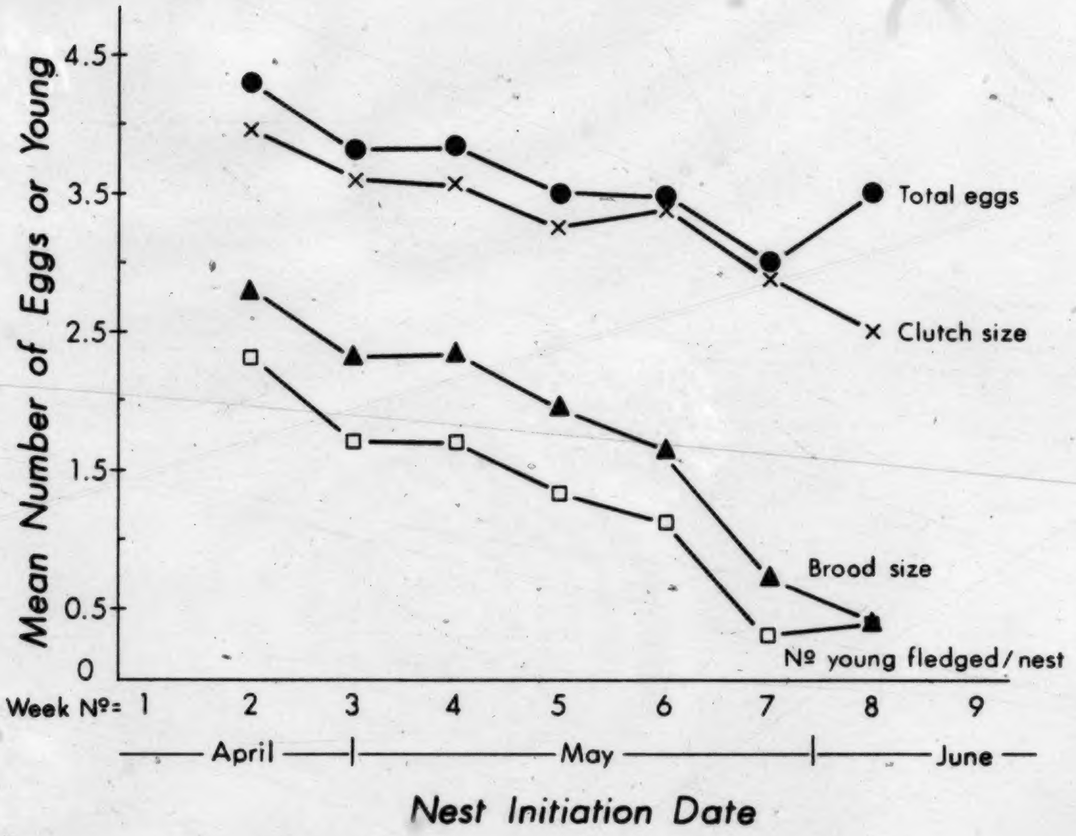


Figure 8 – Comparison of mean reproductive output by nest initiation date, 1979 and 1980.

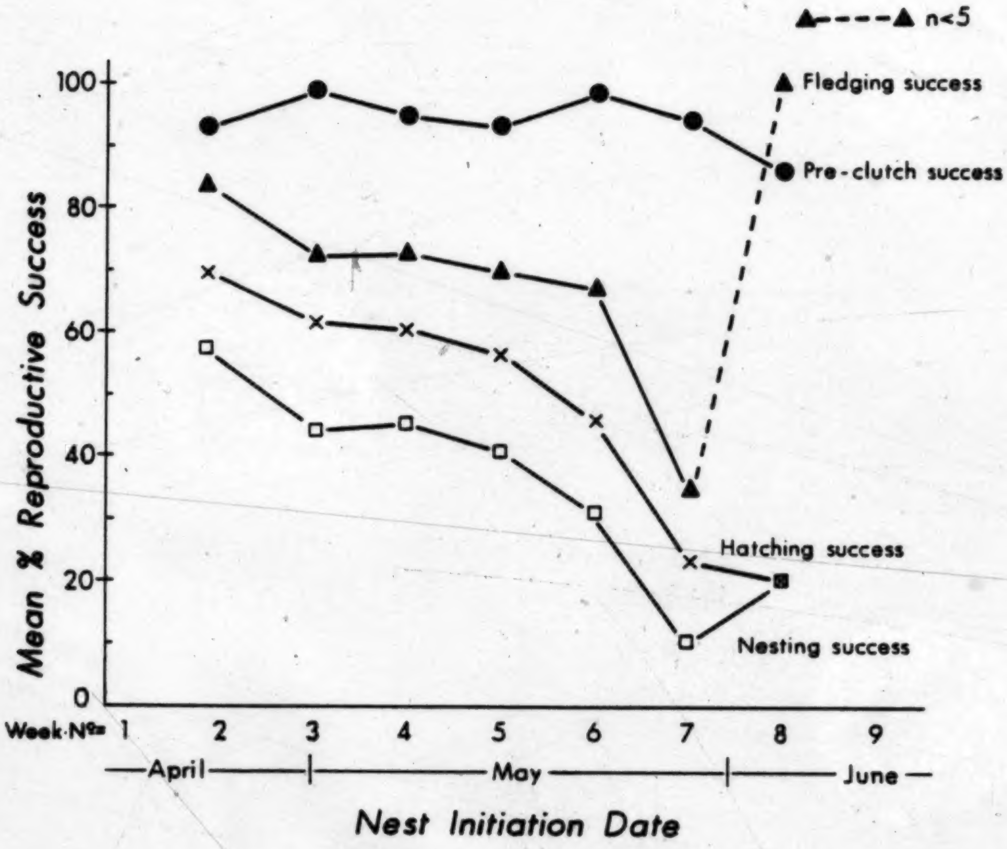


Figure 9 – Comparison of mean reproductive success by nest initiation date, 1979 and 1980.

Although this general trend was consistent in all years studied, a comparison of nest success rates among individual colonies and years reveals several distinct variations (Figure 10). Most difficult to explain among these is the lower fledging rate among nests initiated during the first week of laying at the Newell colony in both 1979 and 1980. This variation cannot be explained by low sample size (n = 21 in 1979, n = 29 in 1980) or by any readily apparent climatic difference between Newell and the other colonies studied. I might speculate that the drastic reduction in early nest productivity in 1979 was, in part, due to the cooler, later spring in that year. If climatic variation is a factor in ultimate fledging rate, then the lower success of nests initiated in week 2 (April 21–28) in 1980 may have been influenced by a short term drop in temperature which occurred in that year between April 20 and 23 (Figure 4). It is difficult to explain, however, why the Tilley South colony had its best nesting success in nests initiated during this week of 1980.

The drastic decline in nesting success on the Hays 1980 colony between weeks two and five is largely due to the unexplained mortality of more than 33% of the young on this colony between June 29 and July 2. This mortality selectively decreased the apparent nesting success of later nests. Many of the larger young which died had attained 18 or more days of age and would therefore have been recorded as fledged. In contrast, many young from later nests had not reached 18 days and were therefore recorded as missing pre-fledglings.

A comparison of variation in reproductive parameters by nest initiation date between years is provided in Figure 11. The general pattern of decreasing reproductive output and success was modified by early season failures in 1979.

Egg Laying

In southern Alberta, egg laying in first nests began in late April and continued until mid to late June annually. New eggs were found in renests, however, until the last week in July. Although there was considerable variation in laying dates among colonies, egg laying occurred significantly earlier in 1980 than in 1979 (Figure 12, MW'U' p = .0000).

The weekly and bi-weekly on-colony observation schedule precludes the calculation of a precise egg laying rate. There were, however, a number of nests in which the laying of a complete clutch took more than seven days. The actual laying rate may therefore be closer to the 1 egg every 2 days reported by Robertson (1971) than the 1

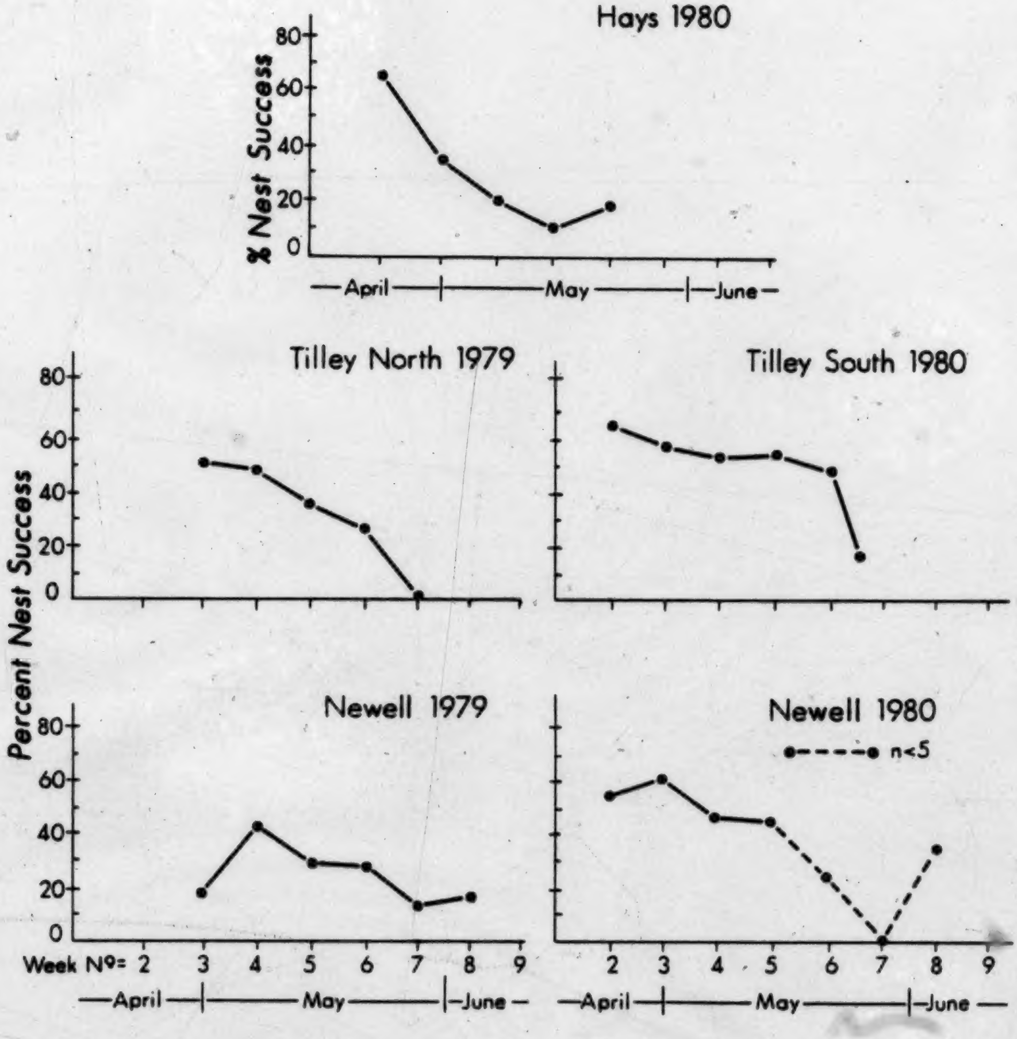


Figure 10 – Comparison of nesting success by nest initiation date at several southern Alberta colonies.

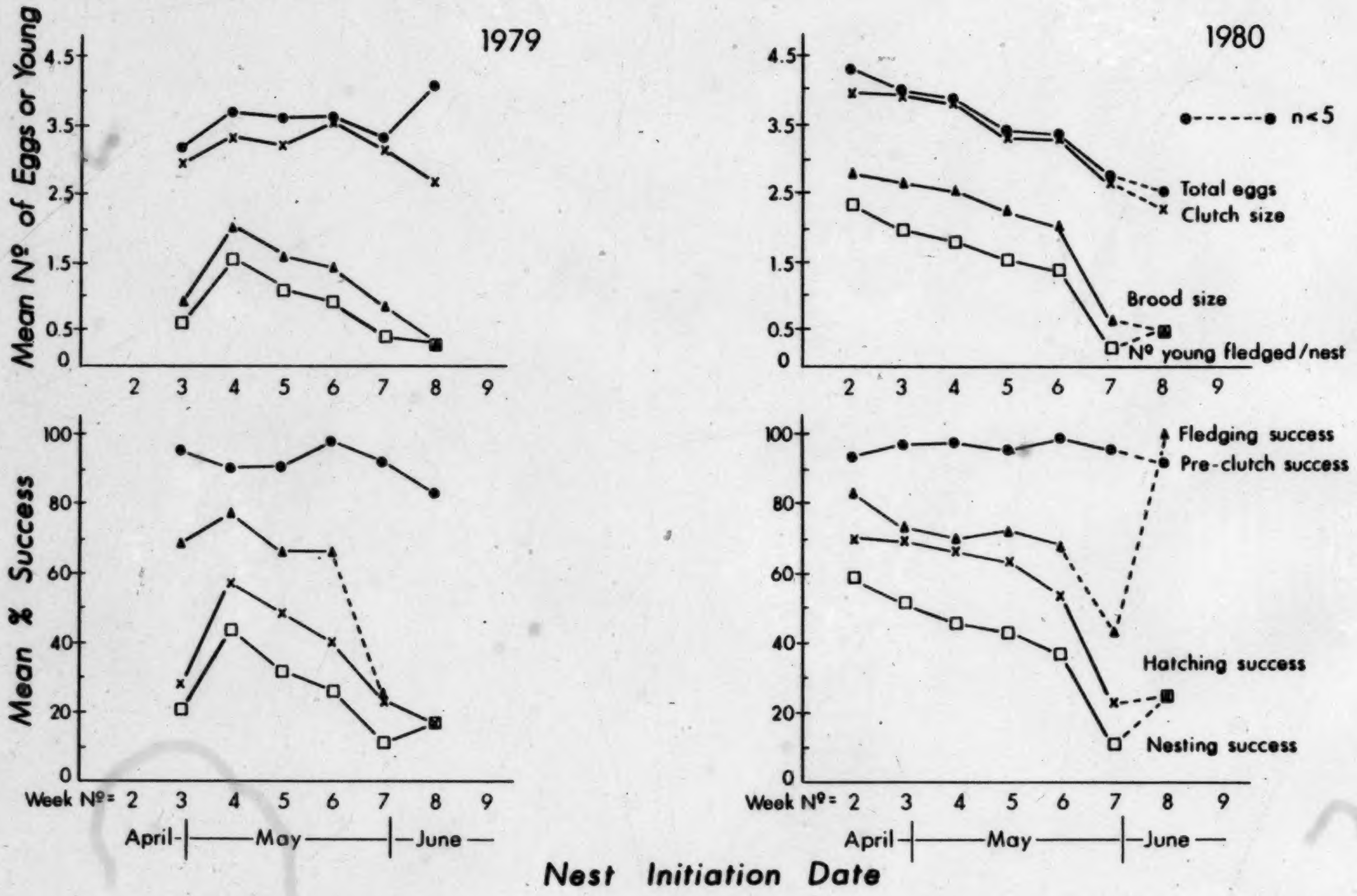


Figure 11 – Comparison of reproductive output and success by nest initiation week between 1979 and 1980.

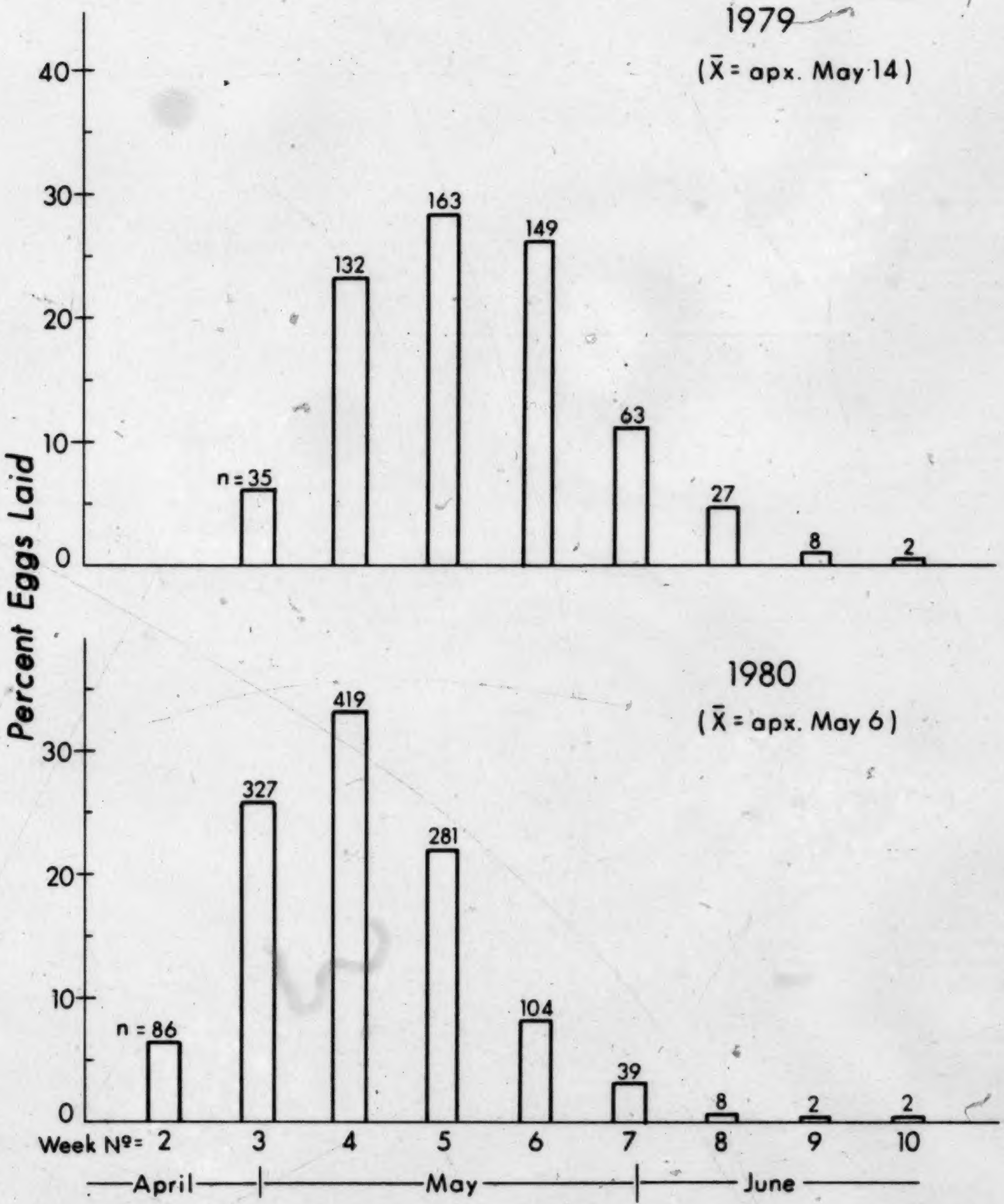


Figure 12 – Distribution of egg laying by week in 1979 and 1980.

egg per day reported by Mitchell (1977), Lewis (1929) and Mendall (1936).

The relative timing of laying between old, large and young, small colonies is similar to that noted for nest initiation and colony arrival data (Figure 13). Cormorants nesting at old, large colonies began laying earlier and ceased laying later in both years studied. The mean laying date on old colonies was significantly earlier than new colonies (MW'U' p = .0000). An examination of these data revealed that the distribution of laying at older larger colonies was skewed to the later part of the season, with the majority of laying occurring in the early season. The newer smaller colonies, by contrast, had a laying pattern which is later and more synchronous.

Pre-clutch Egg Loss

During each visit to a colony, the contents of all marked nests were recorded to obtain estimates of reproductive output and success. For the purposes of this study, clutch size is defined as the maximum number of eggs observed in a nest at any one time.

During intensive observations of the Newell, Tilley and Hays colonies in 1979 and 1980, the sum total of all eggs laid in staked nests during each nesting attempt was also recorded. Pre-clutch egg loss is defined as the difference between the total number of eggs laid and the ultimate clutch size. Egg loss prior to clutch completion occurred in 17% of the nests studied (n = 85). On average, each of these nests lost 1.37 eggs prior to clutch completion (range = 1 to 8 eggs).

The frequency of pre-clutch egg loss did not differ significantly between old and new colonies. Between years, 1979 had significantly more nests showing pre-clutch loss than did 1980 (Chi^2 p = 0.0112). If this greater loss in 1979 was associated with poor spring weather, then one might expect greater losses to occur in the early weeks of nest initiation. In 1979, mean temperature remained below the 1980 level until approximately May 11 (the end of week 4) (Figure 4). When the frequency of pre-clutch egg loss was compared between nests initiated in weeks 1-4 and weeks 5-10, no significant difference was apparent (17.5% vs. 15.9%, respectively, Chi^2 p = 0.6716). When a similar comparison was made between nests initiated during the first week of laying (week 2) and weeks 3-10, pre-clutch egg loss was significantly more frequent in nests initiated in week 2 (26.5% vs. 15.5%, Chi^2 p = 0.0246). It would apear that although mean temperature cannot be directly implicated in pre-clutch egg loss, some factor caused

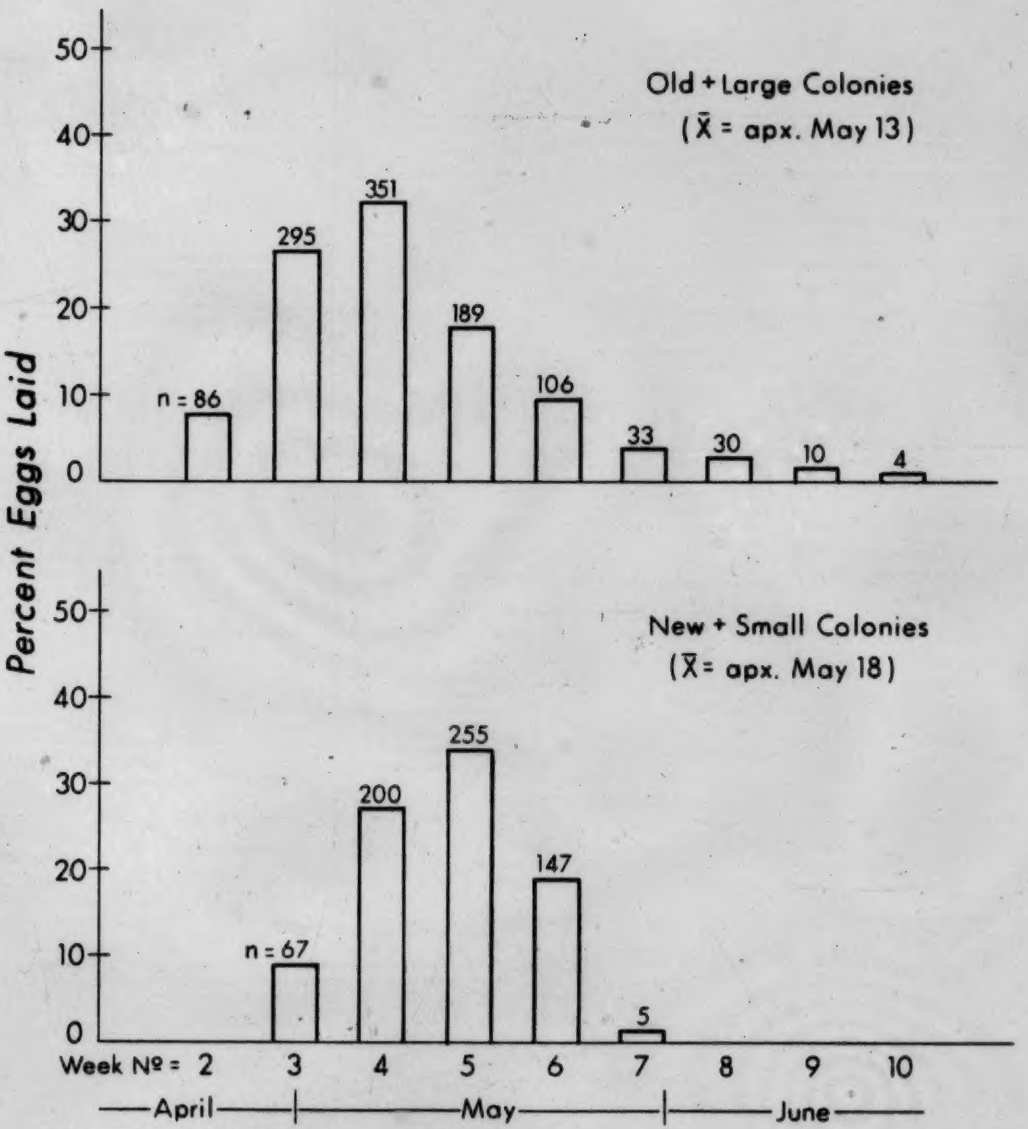


Figure 13 – Comparison of egg laying by week between colony size and age categories.

more pre-clutch loss in nests initiated very early in the season.

The effect that early egg loss had on ultimate clutch size was examined by comparing mean clutch size between nests which lost eggs prior to clutch completion and those which did not. There was a small but significant difference between these two groups with ultimate clutch size being smaller in nests which lost eggs (mean = 3.25 vs. 3.59, MW'U' p = 0.0012). It appears that although Double-crested Cormorants will lay additional eggs to replace those lost early in the season, ultimate clutch size may be decreased in nests where this occurs.

Clutch Size

Clutch size ranged from 1 to 6 eggs with an overall mean of 3.53 (Figure 14). The modal clutch size of four was more frequent than all other sizes combined, and the general distribution was skewed towards lower clutch sizes.

All reproductive success measures increased with increasing clutch size up to the modal size of four (Figure 15). Clutches of five were slightly (5-11%) less successful than four, and although the sample size is small (n = 3) clutches of six were more successful than any other.

No clutch of one produced any young. This may suggest that a single egg is not a sufficiently strong stimuli to induce adequate parental behavior. One-third of these single egg clutches (n = 5) lost one egg prior to clutch completion, while most (n = 10) were the result of a pair laying only one egg. The majority of these nest sites containing a single egg (11 of 14) were later used by renesting cormorants with average success (32% nest success).

A comparison of reproductive output among clutch sizes (Figure 16) revealed that, although reproductive success declined between a clutch size of 4 and 5, the absolute reproductive output (number of young fledged per nest) increased slightly. Initially this would seem to contradict the theory suggested by Lack (1954) that modal clutch size is adapted to the greatest number of young that parents can normally raise. Lack (1966), however, modified this theory to indicate that in expanding populations where environmental limiting factors have not yet been reached, breeding pairs producing larger clutches may be more successful. As this population was expanding rapidly, the increased productivity in larger than modal clutches may be consistent with Lack's clutch

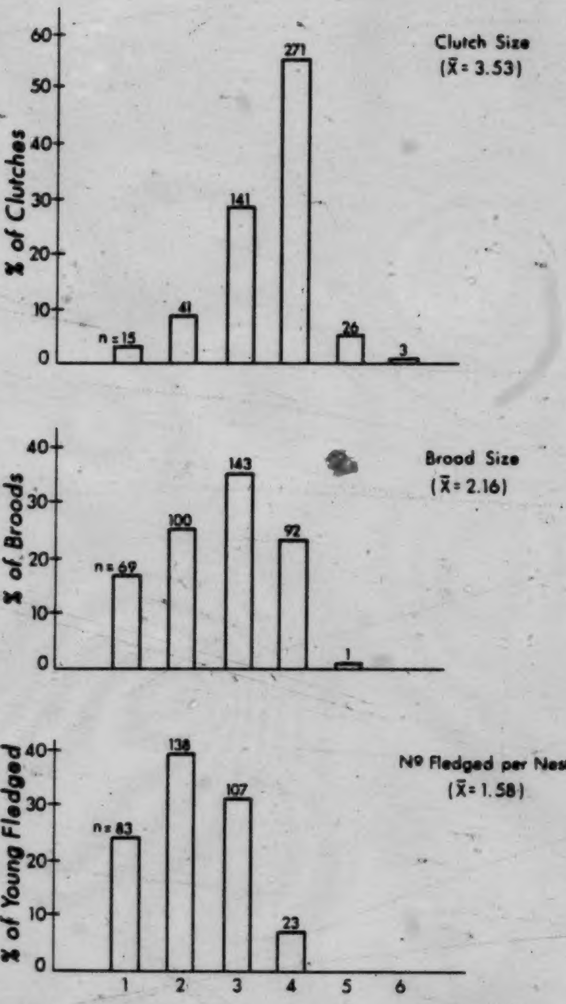


Figure 14 – Frequency distributions of clutch size, brood size and number of young fledged per nest, 1979 and 1980.

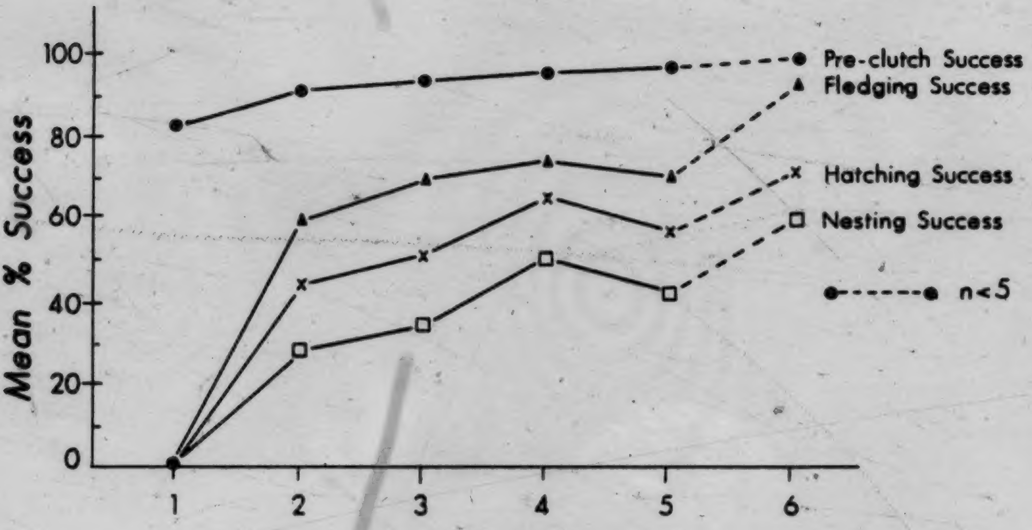


Figure 15 – Variation in reproductive success with clutch size.

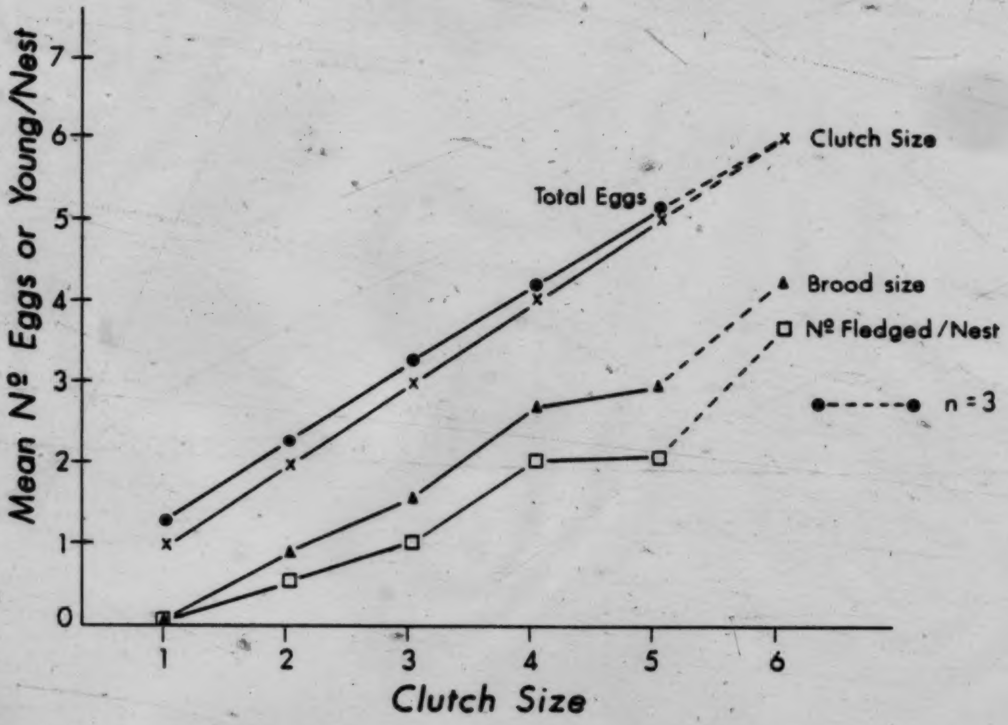


Figure 16 – Variation in reproductive output with clutch size.

size hypothesis.

These data also correspond well with results from artificially enlarged broods of Double-crested Cormorants. Robertson (1971) reported that more young fledged from supra-normal broods than from normal ones. This population was also expanding and was therefore seen to comply with Lack's modified hypothesis (1966).

Clutch size also varied considerably between year and colony types. In the earlier, warmer year of 1980, clutch size was significantly larger than in 1979 (mean = 3.67 vs. 3.23, respectively, MW'U' p = .0000). As pre-clutch egg loss was more common than expected in 1979, this difference might have been due to differential early clutch reduction. If, however, nests which suffered pre-clutch egg loss are removed from the clutch size comparison, the significant difference between years is maintained (MW'U' p = .0000, n = 411).

When I compared clutch size between colony age and size categories, a surprising relationship emerged. Clutch size on old, large colonies was significantly smaller than on new small colonies (3.38 vs. 3.78 respectively, MW'U' p = .0000). This relationship was consistent and significant both within and between years and is difficult to explain. Nests on older colonies are, on average, initiated earlier, and nest initiation date is strongly correlated with clutch size (Figure 8). It appears that although initiation date may influence clutch size, other factors which vary between colony types must also be operating.

Egg Size and Volume

Measurements of the length, width and weight of 448 cormorant eggs were collected in 1980. Southern Alberta eggs are apparently very similar to eggs from other areas in the range of the (*P. a. auritus*) subspecies (Table 1). Although length and width measures are not available, the west coast subspecies *P. a. albociliatus* appears to have heavier eggs.

Of the three measures, egg weight was by far the least consistent. As avian eggs develop they lose weight, decreasing by approximately 18% of their initial weight (Rahn and Ar, 1974). As most eggs were measured only once, egg density (weight divided by volume) was calculated to control for variability in egg size and to compare between different egg ages. A least squares regression comparing egg density by days in the nest

Table 1: Double-crested Cormorant mean egg measurement.

Location	Sample Size	Length (mm)	Width (mm)	Weight (gm)	Source
U.S. Nat. Museum	40	61.60	38.80		Bent 1922
Atlantic Canada	50	59.90	37.70	46.5	Lewis 1929
Maine	15	60.50	37.60		Mendall 1936
Utah-Egg Island	20	59.30	37.10		Behle 1958
B.C.-Mandarte Isl.	215			51.0	Van Tets 1959
Utah	124	60.65	38.80	46.1 (n=20)	Mitchell 1977
Alberta	448	60.74	38.12	44.9	This Study

resulted in a significant regression with the following equation:

$$\text{egg density} = 1.0927 + \text{egg age}\ (-0.005218)\ [n = 146]$$

$$(SE = .0093268) \qquad (SE = .0005186)$$

As the age of an egg increases, its density decreases in a consistent fashion. Using this equation, a cormorant egg would be neutrally buoyant after 17.8 days in the nest (density = 1.0) and would thereafter float in water. Over the average incubation period of 27.19 days, an average egg would decrease in density by approximately 13%.

A documentation of egg size and weight by position in the laying sequence is presented in Table 2. As the relative length and width of eggs varies somewhat independently, egg volume was calculated using the formula developed for southern Alberta cormorant eggs by W. Van Scheik (pers. comm):

$$\text{Volume} = .4985\ LB^2$$

where L = longitudinal axis and B = transverse axis.

Although the sample size was small, egg numbers 5 and 6 were significantly smaller in volume than earlier eggs (MW'U' p = .0199). Although not significant, the first egg in a clutch appeared to be slightly smaller than eggs 2 to 4. There was no significant difference between the egg volumes recorded from new, small vs. old, large colonies (mean = 44.02 vs. 44.55cc respectively, n = 82, 239, MW'U' p = .508).

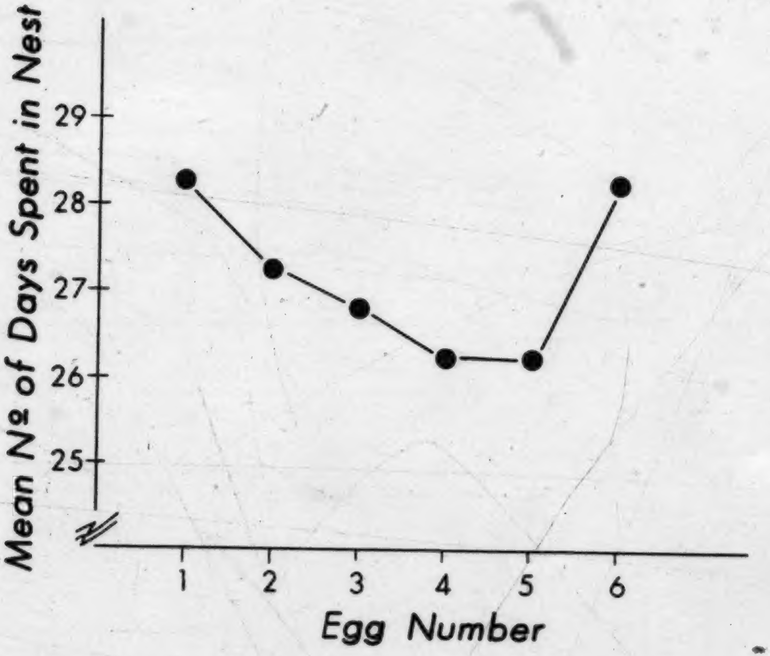
A large percentage (39%) of the eggs used to examine volume and density relationships were collected after rolling or being kicked out of the nest. The possibility that these eggs had been actively rejected by the breeding birds rather than accidentally lost from the nest could not be excluded. If this were true, however, one might suspect that they might be sub-normal in some size or volume character. In fact, eggs which had been kicked from the nest were found to be slightly but significantly larger in volume than eggs from active clutches (mean = 44.81 vs. 43.51cc, n = 177, 258, MW'U' p = .0002).

Incubation

The precise time at which incubation began was not determined, but an estimate can be made by comparing the number of days each egg spent in the nest prior to hatching (Figure 17). As each egg from 1 to 4 spends consecutively less time in the nest, consistent incubation appears to begin near the laying of the fourth egg. On average,

Table 2: Variation in mean egg dimensions between egg number in laying sequence.

Egg #	Sample	Length mm	Width mm	Weight g	Volume cc
1	82	60.9	37.8	44.4	46.05
2	63	60.4	38.3	44.8	46.72
3	54	60.4	38.3	44.6	46.73
4	39	60.0	38.4	43.8	46.73
5	11	59.8	37.7	40.2	44.75
6	3	58.1	36.7	40.0	41.14
Overall	252	60.5	38.1	44.2	46.35



n	=	221	253	244	175	33	7
X̄ Nº Days	=	28.4	27.3	26.8	26.1	26.3	28.6

Figure 17 – Variation in the number of days each egg in a laying sequence spent in the nest prior to hatching.

however, there is less than one day difference between the time eggs 2 to 5 spend in the nest. This suggests that some development and partial incubation may begin sometime after the first egg is layed.

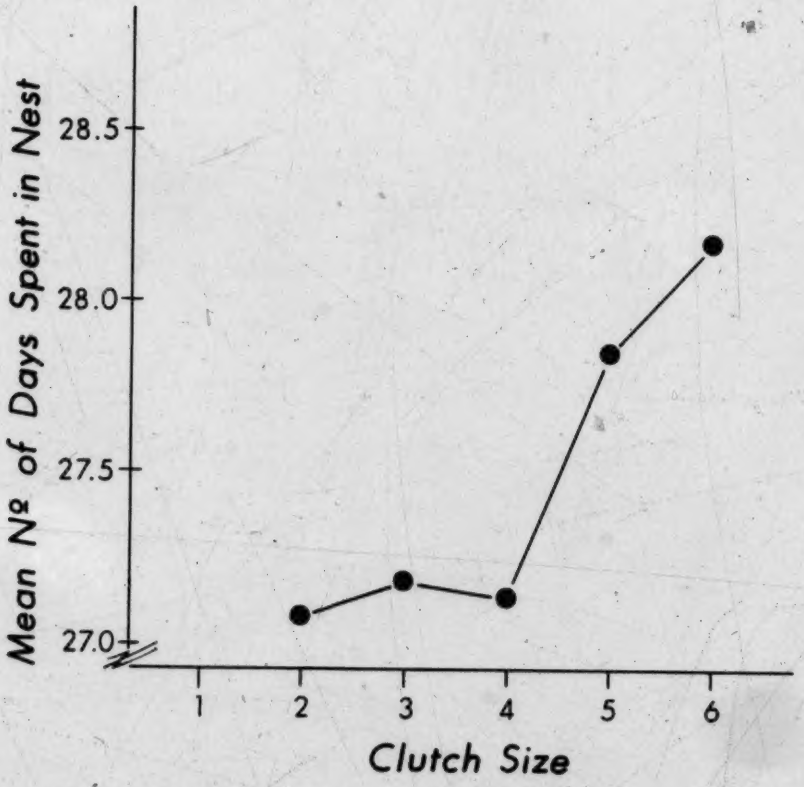
The average in–nest period for all eggs which ultimately hatched was 27.2 days. Infertile or addled eggs, however, often remained in the nest for much longer periods (up to 74 days).

The mean incubation period also varied slightly between different clutch sizes (Figure 18). The mean incubation period for eggs from clutches up to the modal size of 4 remained very close to the overall mean of 27.2 days. Eggs from clutches of 5 and 6, however, showed an increase in incubation period to 27.9 days. Although this difference did not reach statistical significance (MW'U' p = .2516) it may indicate that cormorants have some difficulty incubating large clutches.

Egg Loss

During 1979 and 1980 the ultimate fates of 1657 individually marked eggs were recorded (Table 3). If an egg did not hatch it was recorded as being preyed upon by gulls, kicked (or rolled) out of the nest, crushed in the nest, infertile or addled (more than 35 days in the nest), abandoned in the nest or having disappeared without known reason. As only one clutch was ever recorded as having been abandoned, this category was subsequently removed from analysis. Cases with incomplete histories were also excluded from the data set.

The largest portion of egg loss resulted from the disappearance of eggs from the nest for unknown reasons (n = 413, 59% of all losses). From observations on the colony, I suggest that most of these eggs were removed by predators during our visits. Gulls were occasionally seen flying from a colony with an egg in their bill, but more often eggs were consumed in the nest and the shell removed by the adult cormorant. These eggs were often too fragmented to identify nest or egg number codes and were therefore included in the disappeared category. This category also includes some eggs which were kicked from the nest by adult cormorants and subsequently eaten by gulls, and some which were crushed in the nest but were removed by the adult prior to being recorded.



n =	0	31	183	654	59	11
$\bar{X}$ Nº Days =		27.07	27.19	27.12	27.85	28.18

Figure 18 – Variation in the number of days each egg in various sized clutches spent in the nest prior to hatching.

Table 3: Summary of individual egg fates.

Fate	Percentage	n =
Hatched[1]	57.7%	956
Preyed upon	4.4%	72
Kicked from the nest	4.4%	72
Crushed	1.2%	20
Infertile or Addled	7.4%	124
Disappeared	24.9%	413
Total	100%	1657 eggs

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[1] This figure is based on individual egg histories and should not be confused with hatching success which is brood ÷ clutch x 100.

A comparison of the fate of eggs from old, large colonies versus new, small colonies revealed several interesting relationships. New, small colonies lost a significantly greater proportion of their eggs to predation at the nest (3.3% vs. 5.9%, Chi^2 p = .0213). In old, large colonies, however, significantly more eggs were found to be kicked out of the nest prior to hatching (Chi^2 p = 0.0096). The percentage of infertile or addled eggs was virtually identical in the two colony types (7.5 vs. 7.6%). The number of eggs which disappeared without known cause was also significantly greater in old, large colonies (27% vs. 22%, Chi^2 p = 0.0218). When all egg loss categories were combined, however, there was no significant difference in the proportion of eggs which failed to hatch between the two colony types.

A similar comparison of egg loss between years 1979 and 1980 revealed no significant differences between the number of eggs which were crushed or kicked out of the nest. There were, however, significantly more infertile and addled eggs (9.7% vs. 6.5%, Chi^2 p = .0000), significantly more eggs which disappeared (39% vs. 18%, Chi^2 p = 0.000), and significantly more eggs which were lost to predation (5.1% vs. 4.0%, Chi^2 p = 0.0259) in 1979 vs. 1980.

The ultimate fate of an egg also seemed to be influenced by its relative position in the laying sequence of a particular nest (Figure 19). When a comparison was made between eggs for which the fate is known (i.e., excluding the disappeared category) the first egg laid in any nest failed to hatch significantly more frequently than expected (Chi^2 p = 0.0251). The majority of this loss resulted from higher rates of predation and more frequent loss of an egg from the nest bowl (kicked) (7.9% and 10.1% respectively, Chi^2 p = 0.025 and p = 0.0000 respectively). Although infertile or addled eggs were also more frequent among first eggs (11.6% vs. 10% overall average), this difference was not significant (Chi^2 p = 0.0714).

It might also be expected that the last egg laid in a clutch would be less successful than other eggs. A comparison of last eggs with known fates, however, revealed no significant difference in hatching success (Chi^2 p = .7288) or any of the individual egg loss categories (overall 4 x 2 Chi^2 p = 0.4554). In general, however, hatching success did decrease after the fourth egg layed in a particular nest (Fig. 19). In fact, the frequency of hatching in eggs laid after egg 4 was significantly lower than that

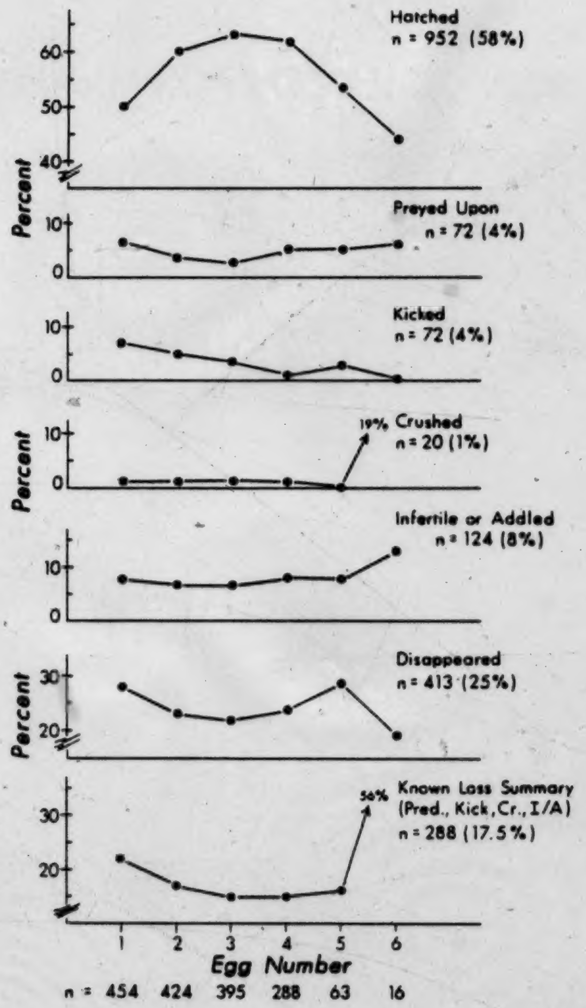


Figure 19 – Variation in egg fate by position in laying sequence.

in eggs 2 to 4 (51% vs. 61%, Chi^2 p = 0.0412).

In examining the decreased hatchability of first and later eggs laid, it was difficult to separate the effects of factors influencing the individual nest (i.e., female condition, parental ability, nest placement, etc.) from the more general influence of laying date (i.e., weather, colony synchrony, etc.) In order to examine this problem, a comparison of egg fate by week in which each egg was laid was carried out (Table 4). For statistical comparison, three categories were established: 1) eggs laid in the first week where laying was recorded (n = 75, 4.6%); 2) eggs laid in weeks 3 through 6 (n = 1431, 87.1%); and 3) eggs laid after week 6 (n = 137, 8.3%). Within these data there was a clearly visible trend towards reduced hatching success in eggs laid early and late in the season. When compared with eggs laid in mid-season (weeks 3 to 6), eggs laid in week 2 and weeks 7-10 were significantly less likely to hatch (Chi^2 p < .0001).

The reasons for this trend are not entirely evident. Although the sample size was small, there was no significant difference between these categories in the frequency of predation, crushed eggs or eggs which were infertile or addled (all Chi^2 values p > .20). There were, however, significantly more eggs kicked from the nest in both week 2 and weeks 7-10 (Chi^2 p < .0001 and p < .01 respectively). The large number of eggs laid after week 6 which ultimately disappeared for unknown reasons also contributed to the decreased hatching success of late season eggs. Significantly more eggs laid after week 6 disappeared than those laid in weeks 3 to 6. Although proportionally more eggs laid in week 2 also disappeared, the difference was not significant (Chi^2 p > .5).

Hatching

Hatching success is defined as brood size divided by clutch size multiplied by 100. This calculation excludes eggs lost prior to clutch completion.

The mean hatching success for the 495 nests studied was 59%, which is extremely close to the 58% hatching success reported by Mitchell (1977) for arboreal cormorants in Utah. No other published records for inland nesting Double-crested Cormorants are available but records from the Pacific coast subspecies show generally higher hatching success (Robertson 1971: 78%; Van Tets 1959: 60%; and Van de Veen 1973: 84%).

Table 4: Egg fate by week in which the egg was laid.

Week	n =	% Hatched	% Preyed Upon	% Kicked	% Crushed	% Infertile or Addled	% Disappeared
2: April 21 to 27	75	41.3	1.3	20	2.7	10.7	24
3: April 28 to May 4	313	67.7	4.2	3.8	1.3	5.8	17.3
4: May 5 to 11	483	64.2	5.4	3.1	0.6	6.2	20.5
5: May 12 to 18	396	54.0	5.3	2.3	1.3	10.6	26.5
6: May 19 to 25	239	61.1	2.5	5	1.7	7.1	22.6
7: May 26 to June 1	92	32.6	4.3	8.7	1.1	7.6	45.7
8: June 2 to June 8	33	21.2	3.0	3.0	3.0	3.0	66.7
9: June 9 to June 15	9	22.2	-	-	-	11.1	66.7
10: June 16 to June 22	3	-	-	-	-	-	100
Total Sample	1643	952	72	72	20	124	403
Overall %		57.9	4.4	4.4	1.2	7.5	24.5

The hatching date for 943 eggs observed ranged from May 25 to July 7, with the mean on June 9. Although Mitchell (1977) did not record a mean hatch date, 90% of the hatching on his Utah colonies was completed by May 30. On my study colonies, 90% of the hatch was completed by June 19.

Both hatching success and mean hatch date vary considerably between colony types and years. As might be expected, the warmer spring year of 1980 had a mean hatch date significantly (4 days) earlier than the cooler year of 1979 (June 7 vs. June 11, MW'U' $p < .0001$). Hatching success was also much greater in 1980 than in 1979 (67% vs. 47%, Chi^2 $p < .0001$).

Hatching success was virtually the same in new, small and old, large colonies (62 vs. 61%). As might be predicted from the earlier discussion of spring return and nest initiation, the mean hatch date was four days earlier on old large colonies (June 7 vs. June 11, MW'U' $p < .0001$). This difference was consistent both within and between years. As initiation date was negatively correlated with hatching success, (Figure 9), it was somewhat surprising that the mean hatching success on the earlier hatching old, large colonies was not higher.

Hatching success also appeared to be related to clutch size. As clutch size increased so did hatching success (Figure 15). Clutch size, in turn, was negatively correlated with nest initiation date, with larger clutches being initiated earlier (Figure 8). These data reinforced the observed trend to higher hatching success in the earlier year of 1980.

Brood Size and Fledging Success

Double-crested Cormorants hatch naked, blind and unable to metabolically or behaviorally control their body temperature (Dunn 1976). Chicks are dependent on adults for temperature regulation until about 14 days of age (Dunn 1976). They generally remain in the nest for 18-21 days, after which they spend increasingly long periods off the nest on their own. Lewis (1929), Mendall (1936), Van Tets (1959) and Mitchell (1977) all provide descriptions of the physical and behavioral developments of Double-crested Cormorant young.

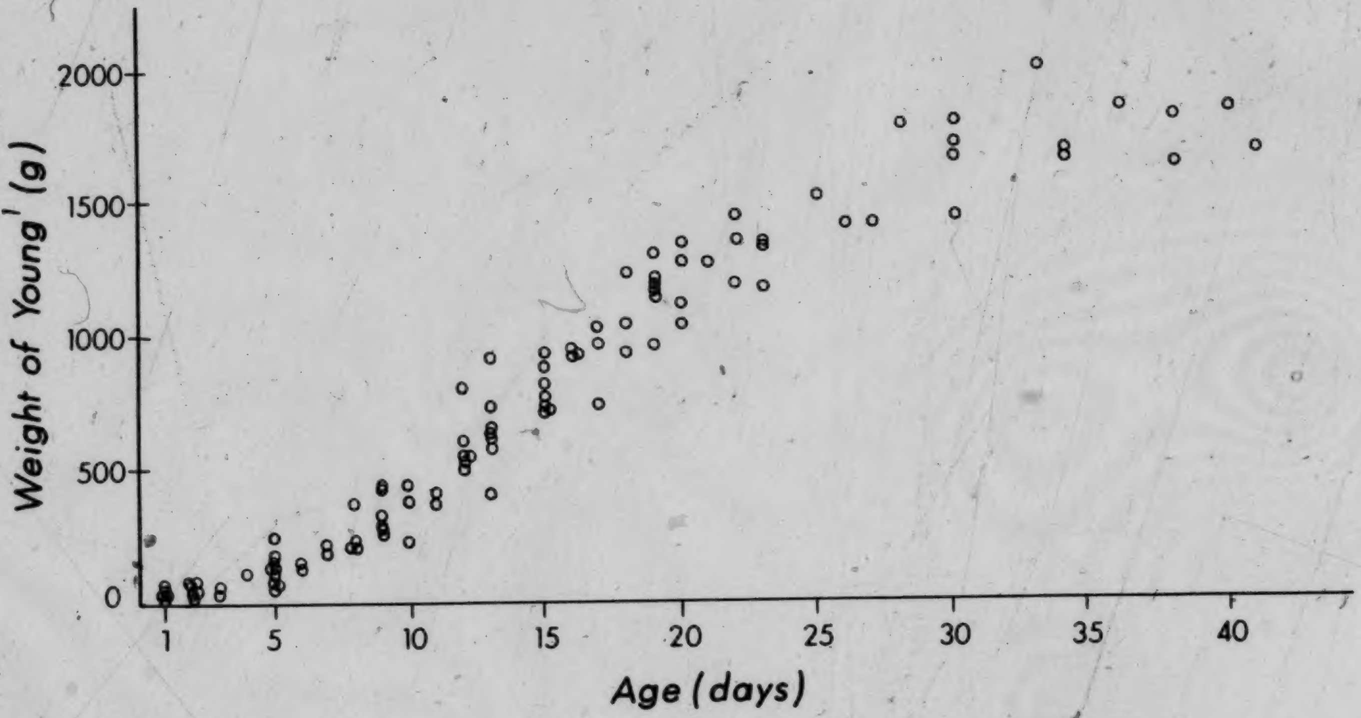
Brood size in southern Alberta ranged from 1 to 5 with an overall mean of 2.16 young per nest (Figure 14). The brood period was defined as the time a nest contains young between 1 and 18 days of age. Excluding renests, this period ranged between May 25, when the first egg hatched, to July 25, 18 days after the last egg hatched. Assuming equal brood survival over time, the mean brood period date was June 27, 18 days later than the mean hatch date. As very few young were individually marked, no more precise dates are available.

The mean fledging success for all colonies and years studied was 73% (n = 399 nests), which resulted in an overall average of 1.58 young fledged per nest (Figure 14). This is somewhat lower than the 1.9 young per nest that Vermeer observed at Lake Newell in 1969, but his was a total count of all young, and may have been inflated by including those which had not yet reached 18 days of age. Mitchell's reported survival for one colony (1977; n = 15) results in a fledging success figure of 72% (13 of 18 young). This compares very well with my data. The particularly low brood size on this colony (mean = 1.06, n = 17 nests) resulted in an average of only 0.76 young being fledged per nest, but Mitchell's overall brood size was considerably larger (2.11, n = 76 nests), and if the fledging success reported was representative, a highly comparable estimate of 1.52 young fledged per nest results.

During 1979, 41 newly hatched cormorant chicks from 14 broods were individually marked. If more than one chick in a nest was found to be untagged, the larger chick was assumed to be the oldest. (In all cases where relative hatching dates were known, this assumption proved valid, n = 5 broods). The survival of these chicks to fledging (18+ days) was subsequently checked during banding and tagging operations. Of the 41 marked individuals, 37 fledged. The young which died during the brood period were all either the last or next-to-last chick hatched in a brood of 3 or 4. It has been previously suggested (Mitchell 1977, Des Granges 1982) that the youngest chicks in a brood may starve after being out-competed by their older and larger siblings for parental feeding.

During 1980, 23 young from 8 broods were individually tagged and weighed every 3 or 4 days until 30 to 40 days old. The weights of individuals which survived provide a growth curve for Double-crested Cormorants in southern Alberta (Figure 20).

More interesting, however, is the comparative growth and survival of brood mates (Figure 21). As in 1979, all of the marked young which died on the colony in 1980



[1] = Only young which survived to June 23 banding were used (n=15)

Figure 20 – Weight growth of nestling Double-crested Cormorants, Tilley South 1980.

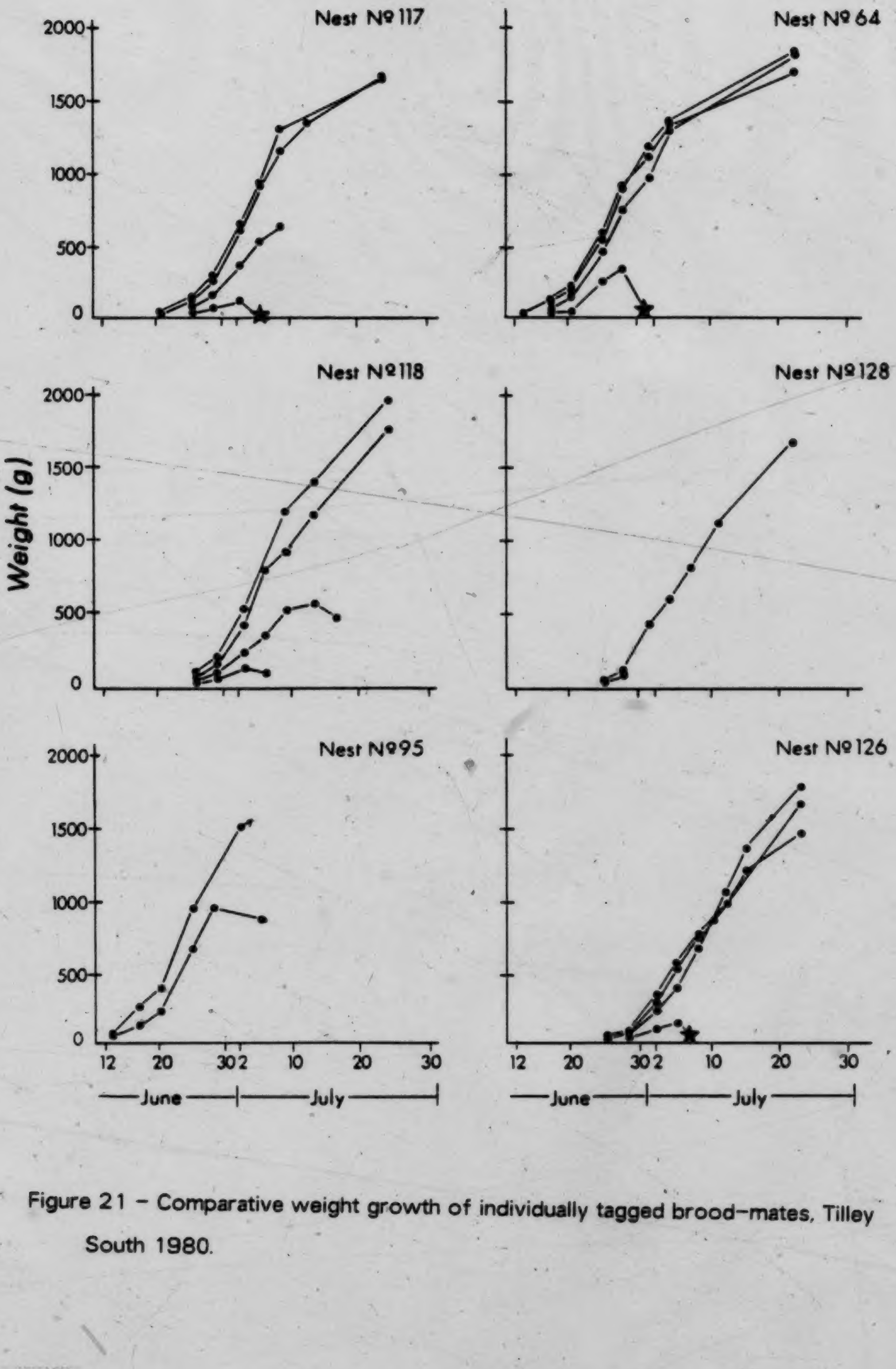


Figure 21 - Comparative weight growth of individually tagged brood-mates, Tilley South 1980.

were the younger, lighter members of broods. In most cases, the rate of weight gain had decreased and in some instances the chicks had begun to loose weight prior to being found dead or disappearing from the colony. In both years, the 3rd and 4th chicks in broods were significantly less likely to survive to fledging than the first and second chicks (1979: Chi² p = 0.0191; 1980: Chi² p = 0.0123).

In 1980, 6 of the 23 tagged chicks died prior to fledging, and two died after attaining 18+ days of age. This.results in a sample fledging success of 74% which is similar to the overall fledging success of 77% for this colony in this year. Survival of the marked sample may therefore be considered as representative of the overall population. The stress associated with handling and weighing does not appear to have differentially affected nestling survival in marked birds.

Brood size also seemed to have an effect on survival to fledging (Fig. 22). The higher mortality of chicks 3 and 4 was reflected in the decreasing fledging success of larger broods. It is, however more difficult to explain why broods of one have the lowest fledging success. If nestmate competition and/or limited feeding ability were the major factors causing brood mortality, single chick broods might have been expected to have the highest fledging success. In contrast, my data indicated that broods of one were significantly less successful than broods of two (Chi² p = .0152). Although the difference did not attain significance, broods of one were also less successful than all other broods combined (Chi² p = 0.0556).

Although fledging success was lowest in small and large broods the absolute number of young fledged per nest increased with increasing brood size (Fig. 23). It appears that brood size overrides the differences in fledging success when reproductive output is measured.

As would be expected, the larger clutches found in 1980 vs. 1979 were translated into significantly larger broods (mean = 1.53 vs. 2.47 MW'U' p = .0000). Although fledging success was not significantly different between years (Chi² p = .7611), this difference carried through to result in a significantly greater number of young fledged per nest in 1980 (1.11 vs. 1.82, MW'U' p = .0000).

A similar consistency was found in the relation between new, small vs. old, large colonies. Clutch size, brood size and number of young fledged per nest were all

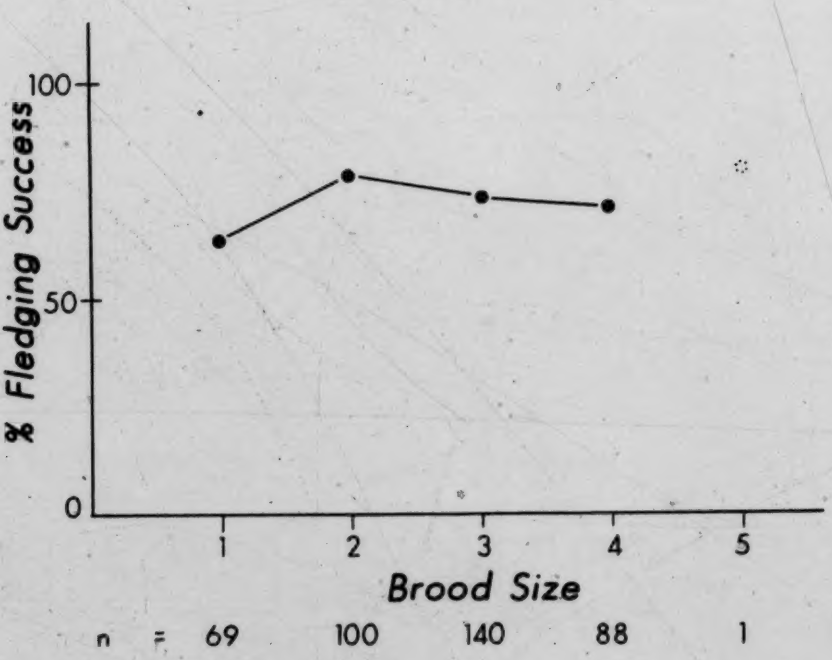


Figure 22 – Variation in fledging success with brood size.

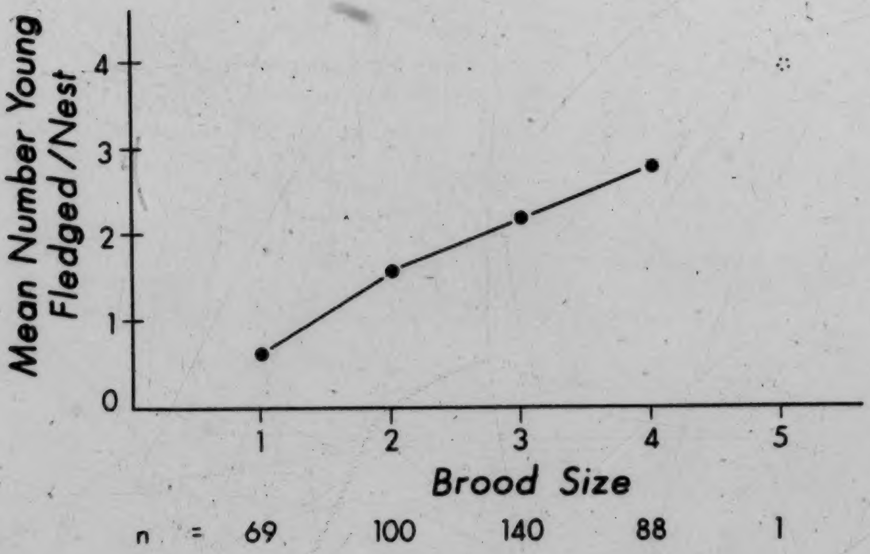


Figure 23 – Variation in the number of young fledged per nest with brood size.

significantly higher in new, small colonies (Clutch MW'U' p = .0000, brood MW'U' p = .0280; fledge MW'U' p = .0056). In this case, however, new, small colonies also had significantly greater fledging success than old, large colonies (70.5 vs. 76.0%, Chi² p = .0512).

Late Season Colony Use

Although Double-crested Cormorants utilized the colony islands until their fall departure, their pattern of use changed as the young grew older and more self-reliant. For the first two to three weeks after hatching, the young remained in the nest and were almost always accompanied by an adult. As the young became more mobile, they made short excursions out of the nest but returned for feeding and, in the evening, to be brooded. By late June to early July most young were 3-4 weeks old and were left unattended on the nest during the day.

During July the attachment of both young and adults to the nest site slowly decreased. The adults were first to show this trend, spending progressively less time with their young on the nest and more time on other areas of the colony or away from the nesting island. The aggressive and persistent food-begging of the larger young undoubtedly contributed to the increasing absence of adults. By the third week in July, large numbers of young were also spending most of the day away from their nests; loafing on shorelines and other open areas of the colony.

By late July to early August, most nest sites were abandoned during the day. Young were fed wherever they were found by returning parents, most often on shorelines and open spaces near the nests. Adults were often pursued by hungry young around the colony and into the water. Although Mitchell (1977) reported never seeing young fed on the water, I frequently observed that young which chased their parents into the water were fed there.

A large sample of young fledged from southern Alberta colonies in 1978 through 1980 were banded prior to attaining flight (Table 5). A reasonable estimate of post-banding on-colony mortality may be derived by examining the number of banded dead young found on each colony (Table 6). The overall value of 4.8% is a minimum estimate of pre-flight late season mortality. Some banded young may have died on the colony and not been found, and in at least one year, many young died on a colony prior to

Table 5: Total number and percentage of young cormorants banded on southern Alberta colonies: 1978 to 1980.

Colony	1978 #Banded	1978 %Total[1]	1979 #Banded	1979 %Total[1]	1980 #Banded	1980 %Total[1]	Overall #Banded	Overall %Total[1]
Newell	591	65[2]	569	85[2]	492	35[2]	1652	56
Hays	218	46[3]	407	96[4]	393	100[4]	1018	79
Tilley North	69	99[4]	83	97[4]	No Young		152	97
Tilley South	34	100[4]	41	65[4]	246	93[4]	321	91
Total	912	61%	1100	92%	1131	55%	3143	66%

[1] Number chicks banded ÷ total number of young available x 100

[2] Estimate of total young = number of active nests X mean number fledged per nest

[3] Estimate of total young from June 2 total count + (number of eggs X 0.424) [0.424 = mean nesting success]

[4] Estimate of total young from late season count (near July 15) + correction for eggs still in nests as above

Table 6: Minimum post-banding on-colony mortality of Double-crested Cormorants in southern Alberta.

	1978			1979			1980			Overall		
	Dead	Banded	%	Dead	Banded	%	Dead	Banded	%	Dead	Banded	%
Newell	50	591	8.5	22	569	3.9	24	492	4.9	96	1652	5.8
Hays	6	218	2.8	18	407	4.4	4	393	1.0	28	1018	2.8
Tilley North	10	69	15	2	83	2.4	0	0	0	12	152	7.9
Tilley South	7	34	21	0	41	0	9	246	3.7	16	321	5.0
Total	73	912	8.0%	42	1100	3.8%	37	1131	3.3%	152	3143	4.8%

being banded (Hays, 1980). So many factors influenced this estimate between different colonies and years, that no statistical comparisons were made.

Young Double-crested Cormorants were often observed swimming prior to attaining flight. In fact, in 1978 some mortality resulted when 4-6 week old chicks were allowed to swim away from the colony island during a data collection visit. Some of these young were later found dead or dying on the shore of the colony. Those which were alive were very weak and thoroughly wet, and were thought to be suffering from exhaustion or hypothermia. Subsequent to this, young chicks were prevented from escaping to the water.

By early August the abandoned nests were often used as loafing areas for adults, while the young loafed in groups near the shore. Younger chicks returned to their nests during the evening to be brooded or fed. It was also common, particularly at the Newell colony, to observe nest structures used for mock courtship, nest building and nest defence by non-breeding subadults and, less frequently, by young of the year. In 1978 on the Newell colony this type of behavior continued from early August until late September, shortly before the colony was abandoned. At the smaller Tilley North colony, subadults were considerably less common and this type of behavior was infrequently observed.

Although the precise age at which flight was attained was not documented, young of the year were first observed in extended flight in late July to early August, between approximately 8 and 9 weeks of age. These flights were preceded by a period of practice which included flapping into the wind and/or gliding from island edges to the water or land below.

By late August, both adults and fledged young were found loafing and roosting on islands and points away from the nesting colony. On many lakes this process continued until cormorants were found on the lake but none remained on the colony. The temporal pattern of fall colony abandonment was monitored in both 1978 and 1980 and was generally the reverse of spring arrival, with the small colonies (Tilley North & South, Little Bow and Barkhausen) being abandoned by early to mid-September. Data from the large colony on Hays Reservoir was difficult to obtain as tall herbaceous vegetation blocked the view of the colony site. It appeared, however, that although cormorants remained on the reservoir until mid to late September, they abandoned the nest sites and colony island by late August.

During September, while all other colonies were decreasing in a relatively consistent manner, the Newell colony showed an increase in the number of cormorants present. This increase suggested that Lake Newell was being used as a staging area prior to fall migration. A portion of this apparent increase, however, may also have been due to rising water levels which forced loafing birds onto a gravel bar which was more visible from the observation blind. Only in 1979 did the total number of cormorants on the island exceed the number of adults and young which could be estimated from the number of active nests and mean number of young fledged per nest.

In all years color marked young of the year from other colonies were observed on the Newell colony during August and September, often after their natal colony was abandoned for the year (Table 7). Only the Tilley North colony was observed with comparable frequency and accuracy during 1978 and 1979. During these years, however, no banded young from other colonies were ever observed at Tilley North. Although there appeared to be some pre-migratory dispersal among young of the year, with the exception of the Newell observations, only one banded fledgling was observed to visit another colony prior to fall departure (1 Newell young of the year observed at Barkhausen in 1978).

In all years the Newell colony was the last to be abandoned (Table 8). In both 1978 and 1980, when late season observations were continued into October, cormorants abandoned the Newell colony in the second or third week of October. On average, this is 4 to 6 weeks later than the last birds were observed on other southern Alberta colonies.

It should be noted that Double-crested Cormorants were often observed on other areas of colony lakes for several weeks after the nesting island was abandoned. When these observations were compared, cormorants still remained at least two weeks later and in much larger numbers on Lake Newell than on the other waterbodies.

Renesting

In a study such as this, where breeding birds are not individually marked, renesting is very difficult to document. It is never positively known whether the late nesting attempts, following an initial failure, are in fact a renesting attempt by one or both of the

Table 7: Observations of color marked young of the year from other colonies at Pelican Island, Lake Newell.

Date	YEAR 1978	1979*	1980**
Aug. 8-14		1-Hays	
Aug. 15-21	1-Little Bow, 1-Hays		
Aug. 22-28	2-Hays, 2-Little Bow		
Aug. 29-Sept. 4			
Sept. 5-11	1-Little Bow, 1-Hays, 1-Tilley North		
Sept. 12-18	1-Tilley North		
Sept. 19-25	1-Little Bow		
Sept. 26-Oct. 2	1-Little Bow	4-Hays	
Oct. 3-9			1-Hays
Observation Periods	18	11	8

* Little Bow = inactive in this year

** Tilley North = inactive in this year

Table 8: Date last D-c Cormorants were observed on southern Alberta colony islands.

Colony	1978	1979	1980
Newell	Oct. 10[1]	> Sept. 29[2]	> Oct. 13[2]
Hays	Sept. 3[1]	< Sept. 14[3]	Aug. 24[1]
Tilley North	Sept. 3[1]	~ Sept. 3[1]	Early August[4]
Tilley South	< Sept. 9[3]	~ Sept. 4[1]	~ Aug. 20[1]
Little Bow	July 29[1]	~ June 30[1,4]	< Aug. 21[3]
Barkhausen	Sept. 13[1]	> Aug. 22[4]	< Sept. 10[3]

[1] = midpoint between last observation of cormorants on colony and first observation of colony abandoned.

[2] > = observations terminated before colony totally abandoned.

[3] < = insufficient August observations to determine exact date. Colony abandoned prior to date indicated.

[4] = all nests abandoned prior to hatching, no young produced.

same pair, or a late nesting attempt by a new pair using a previously established nest.

Renesting was assumed to be a second (or third) nesting attempt by the same pair in the same nest. Of the 60 renests observed, 58 were second attempts and 2 were third attempts following 2 previous failures.

When compared with first nests, renesting cormorants produced smaller numbers of eggs and young, and were significantly less successful at hatching and fledging the eggs and young produced (Table 9). As would be expected, renests were also initiated much later than first nests. The mean nest initiation date for renests was June 21, 42 days later than for first nests.

Most of the renesting attempts followed the failure of first nests. In 14 of the 58 cases, however, the first nest occupants had raised young to fledging (18+ days) prior to renesting. In these cases it was assumed that the original young were lost after 18 days, thus providing the stimulus to the breeding pair to renest. Only 1 of these 14 renesting pairs was successful in fledging a second brood from the same nest.

As was mentioned in the main nest initiation section, renests were not evenly distributed. There was a strong and significant trend for renests to be concentrated in the old, large colonies rather than in new, small ones (Chi^2 $p = 0.0003$). In addition, of the 6 renesting attempts which were documented in new small colonies, none were successful at fledging young. In contrast, 20% (11) of the 54 renesting pairs on old, large colonies succeeded in fledging young.

Contrary to what might be expected from the lower nesting success observed in 1979, renests were not significantly concentrated in 1979 over 1980. Similarly, successful renests were not significantly concentrated in either year.

In first nests, the initiation date was negatively correlated with all reproductive output and success measures (Figure 8 and 9). A similar relationship was not apparent for renests (Fig. 24). Mean success remained below 14% for all two week periods observed (weeks were clumped to increase sample size), and mean clutch size increased only slightly over the period studied.

The physical dimensions of 17 eggs from 7 renest clutches were recorded in 1980. It was somewhat surprising to find that eggs in renests were significantly heavier, wider and of greater volume than those recorded from first nests (Table 10). Although

Table 9: Comparison of reproductive output and success between first nests and renests.

	First Nests		Renests		
	mean	n =	mean	n =	Difference
Nest Initiation	May 10	496	June 21	60	42 days
Total Eggs	3.76	496	2.65	60	1.11*
Clutch Size	3.53	496	2.52	60	1.01*
Brood Size	2.16	495	0.77	60	1.39*
# Fledged per Nest	1.58	489	0.32	60	1.26*
Hatching Success	61.2%	489	30.6%	60	30.6%**
Fledging Success	73.2%	489	41.6%	60	31.6%**
Overall Nest Success	44.8%	489	13.0%	60	31.8%**

* MW'U' $p < .001$

** Chi^2 $p < .0001$

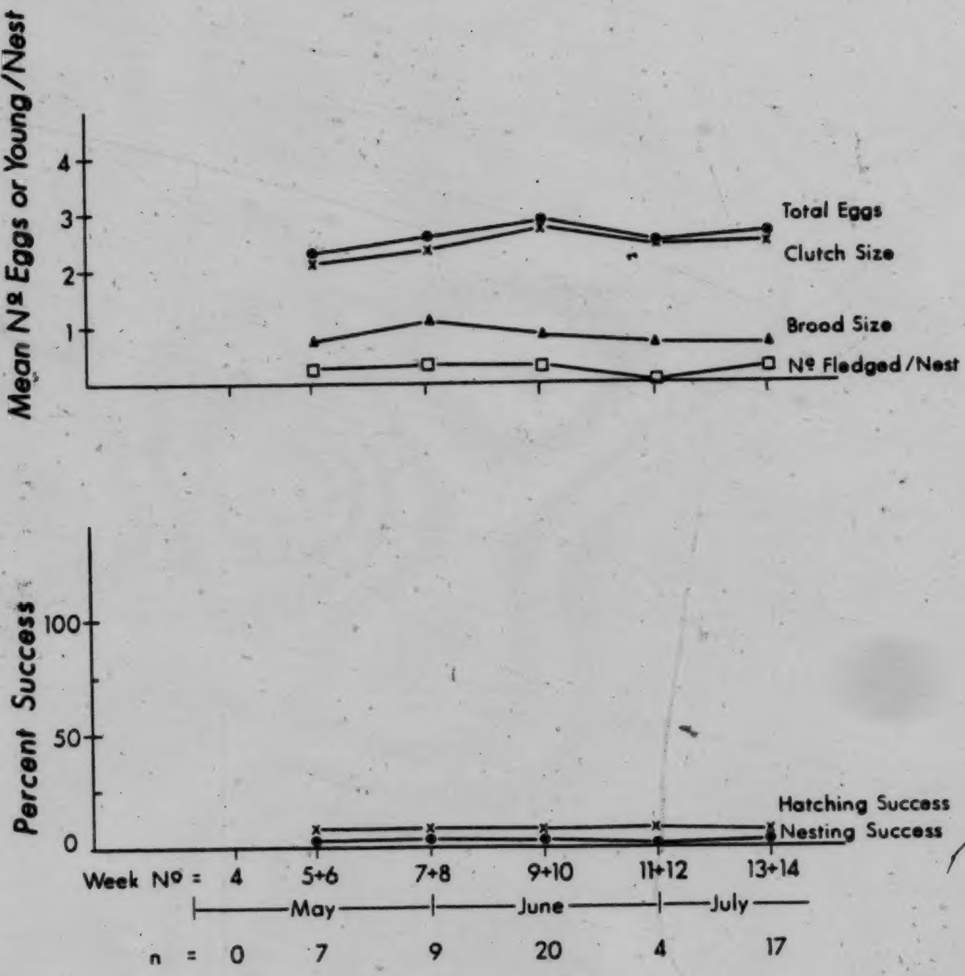


Figure 24 – Variation in reproductive output and success of renests by initiation week.

Table 10: Physical dimensions of eggs from first nests and renests.

	First Nests	Renests	Difference[1]
Length (mm)	60.5	60.4	p = .6311
Width (mm)	37.9	38.8	p = .0091
Weight (g)	441	469	p = .005
Volume (cc)	45.91	47.89	p = .036
n =	258	17	

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[1] Significance tested with MW'U'

the sample size was small, it would appear that the decline in renesting success was not clearly attributable to gross changes in the ability to produce eggs.

B. The Effect of Nest Site Parameters on Reproductive Output and Success

During the course of this study, I collected information on a variety of nest site parameters which I suspected might influence or indicate differences in reproductive parameters. The nest itself was described by measuring its diameter and height. The relative placement of a nest within the colony was categorized as being either central or peripheral and the minimum distance to the next nest was measured. When possible, the relative age of the nest structures was recorded.

These data were compared in two general ways. By examining how nest initiation date varied with these nest parameters, some indication of habitat choice by returning cormorants was obtained. A further comparison of reproductive output and success between different nest types provided insight into the relative quality of different habitat types and/or the individuals occupying them.

Central vs. Peripheral Nests

A summary of comparative reproductive and nest parameter data for central and peripheral nests is presented in Table 11.

On average, central nests were established 7 days earlier than peripheral nests. Nesting generally began on the more central portions of any particular subcolony and proceeded to the more peripheral areas. This pattern was particularly well documented in the nest establishment pattern of subcolony 1 on Tilley South in 1980 (Figure 7).

This pattern was less consistent in new subcolonies established later in the season (i.e., Figure 7, subcolony 2), where new nests were often appended to one end of the existing nest group, resulting in a more linear pattern of growth. This may be a response to decreased conspecific interference from recently established nests on one colony end. Qualitative observations indicated that breeding birds on further advanced, older portions of the colony were considerably less tolerant and more aggressive toward adjacent courting birds. Knopf (1979) attributed similar variation in both the pattern and size of White Pelican (*Pelecanus erythrorhynchos*) colonies in Great Salt Lake to similarly conflicting tendencies towards gregariousness and social intolerance.

Although mean clutch size was very similar in central and peripheral nests, brood size was slightly larger and the greater number of young fledged per nest in central nests approached significance (MW'U' p = .0544). These differences were generated by

Table 11: Comparison of reproductive data, nest parameters and egg fate between central and peripheral nests

	Central		Peripheral		
Nest Data	Mean	n =	Mean	n =	Difference
Nest initiation	May 5	173	May 12	290	p = .0000[1]
Total eggs	3.88	173	3.69	291	p = .0528[1]
Clutch size	3.58	173	3.54	291	p = .8320[1]
Brood size	2.32	173	2.17	390	p = .3282[1]
# Fledged per nest	1.77	170	1.54	288	p = .0544[1]
Pre-clutch success	92.3%	170	95.9%	288	p = .0011[2]
Hatching success	64.8%	170	61.3%	288	p = .1573[2]
Fledging success	76.3%	170	70.9%	288	p = .0621[2]
Nest success	49.4%	170	43.5%	288	p = .0199[2]
Fall nest height	20.1 cm	167	19.2 cm	271	p = .0720[1]
Nearest neighbour	70.7 cm	167	73.6 cm	270	p = .0010[1]
New: Reused nests	30: 127		127: 146		p = .0000[2]
Egg Fate: Hatched	60.0%	343	59.1%	577	p = .7435[2]
Preyed upon	5.6%	32	4.0%	39	p = .1468[2]
Kicked	4.9%	28	3.0%	29	p = .0524[2]
Crushed	1.9%	11	0.9%	9	p = .0923[2]
Infertile/Addled	7.2%	41	7.7%	75	p = .7094[2]
Disappeared	20.5%	117	25.0%	244	p = .0412[2]

[1] Significance tested with MW'U'

[2] Significance tested with Chi^2

greater hatching and fledging success, resulting in significantly greater overall nesting success in central nests (Table 11).

On average, however, more eggs were layed in central nests to attain the equivalent clutch size of a peripheral nest. Pre-clutch egg loss was significantly higher in central nests (7.7%) than peripheral nests (4.1%).

It would appear that breeding pairs occupying central nests suffered greater early egg loss but were more successful at converting completed clutches into fledged young. In contrast, peripheral nesting pairs suffered lower pre-clutch mortality but were less able to produce young once clutches were complete.

It was difficult to determine how much of the apparent difference in reproductive parameters between central and peripheral nests was due to nest location per se as opposed to the differences in nest initiation date. To examine this question, the year was divided into early and late periods at May 10, the mean nest initiation date. The two nest types were then compared within and between these temporal groups (Table 12). Within both early and late periods, central nests were initiated significantly earlier than peripheral sites. The general trend toward greater production in central nests observed in the overall data, however, was not significant within the early or late period. Although fledging success was significantly greater in central nests during the early period, overall nest success was not significantly different in either portion of the year. The pattern of greater egg loss prior to clutch completion in central nests was, however, significant in both the early and late periods.

In an attempt to control for the effect of initiation date, early peripheral nests were compared with late central nests. If habitat related characteristics were of primary importance, one would expect that late central nests would maintain their overall superiority over early peripheral sites. This did not occur. Early peripheral nests had significantly larger clutches and were numerically greater in all other output and success measures.

When the fates of individually marked eggs were compared, the only significant difference was the larger percentage of eggs disappearing from peripheral nests. This difference was balanced by slightly larger known losses from central nests; resulting in very similar hatching success between these two nest types (Table 11).

Table 12: Comparison of reproductive output and success between early and late central and peripheral nests.

	Early (≤ May 10)					Late (> May 10)					
	Central Mean	n =	Peripheral Mean	n =	Difference	Central Mean	n =	Peripheral Mean	n =	Difference	Comparison of Early Peripheral vs. Late Central
Nest Initiation	May 2	125	May 5	124	p = .0000[1]	May 15	48	May 17	166	p = .0005[1]	p = .000[1]
Total eggs	4.02	125	3.87	124	p = .3231[1]	3.50	48	3.56	166	p = .7215[1]	p = .0205[1]
Clutch size	3.70	125	3.66	124	p = .6917[1]	3.27	48	3.45	166	p = .3683[1]	p = .0114[1]
Brood size	2.42	125	2.43	123	p = .8393[1]	2.04	48	1.96	166	p = .7307[1]	p = .1112[1]
# Fledged per nest	1.93	124	1.75	122	p = .2751[1]	1.35	46	1.38	166	p = .9047[1]	p = .0537[1]
Pre-clutch success	92.0%	124	96.8%	122	p = .0013[2]	93.4%	46	16.9%	166	p = .0408[2]	p = .0603[2]
Hatching success	65.4%	124	66.4%	122	p = .7521[2]	62.4%	46	56.8%	166	p = .2199[2]	p = .3679[2]
Fledging success	79.7%	124	72.0%	122	p = .0272[2]	66.2%	46	70.4%	166	p = .4364[2]	p = .2823[2]
Nest success	48.0%	124	46.3%	122	p = .1915[2]	41.3%	46	40.0%	166	p = .7747[2]	p = .1649[2]

[1] Significance tested with MW'U'

[2] Significance tested with Chi^2

Central nests were also slightly higher and slightly but significantly closer together than peripheral nests. The ratio of new to reused nests also differed significantly, with central nests being 81% reused and peripheral nests only 53.5% reused (Table 11).

Comparative Nest Height

In the early spring of each year, prior to or soon after the return of cormorants to their nesting colonies, each numbered nest was categorized as being low (0 to 15 cm) medium (16 to 30 cm) or high (> 30 cm). In the fall of each year, the absolute height of each staked nest was also recorded. I found that nest height increased with nest age (Figure 25). During the early years of the study, nest height class was used as an indirect measure of nest age.

Cormorants returning early to my study colonies selected taller nests. The mean nest initiation date was 5.1 days earlier on high than medium nests, and 4.5 days earlier on medium than low nests (Table 13).

A consistent pattern emerged when reproductive output parameters were compared. In all cases, high nests were more productive than medium or low nests (Table 13). With the exception of mean brood size, medium nests were consistently more productive than low nests. When these differences were tested, however, only the greater brood size and number of young fledged per nest in high vs. medium nests attained significance.

A similar pattern was found when reproductive success measures were compared. With the exception of pre-clutch success, high nests were more successful in all stages of reproduction than either medium or low nests. The differences between medium and low nests, however, were less consistent. Medium nests had better fledging success but poorer hatching success than low nests, resulting in very similar overall nesting success.

The above analysis compares reproductive data by spring nest height class. Although a small number of nests in the low category may have been newly built in the year studied, the vast majority of these data relate to reused nest structures.

Nest Age

Several authors have suggested the possibility that the reuse of previously built nest structures may provide some reproductive advantage (Snow 1960, Mitchell 1977,

Table 13: Comparison of reproductive data and nest site parameters between spring nest height categories

	High (> 30cm)			Medium (16-30cm)			Low (0-15cm)		
	Mean	n=	High vs. Med.	Mean	n=	Med. vs. Low	Mean	n=	High vs. Low
Nest initiation	May 2	80	$p = .0000^1$	May 7	180	$p = .0000^1$	May 12	92	$p = .0000^1$
Total eggs	3.93	81	$p = .3729^1$	3.81	180	$p = .3447^1$	3.67	92	$p = .0983^1$
Clutch size	3.64	81	$p = .3389^1$	3.54	180	$p = .5421^1$	3.47	92	$p = .1795^1$
Brood size	2.46	81	$p = .0308^1$	2.10	179	$p = .3397^1$	2.24	92	$p = .2687^1$
# Fledged per nest	1.87	71	$p = .0440^1$	1.49	176	$p = .8806^1$	1.48	91	$p = .0527^1$
Pre-clutch success	92.6%	71	$p = .8767^2$	92.9%	176	$p = .3196^2$	94.6%	91	$p = .3273^2$
Hatching success	67.6%	71	$p = .0213^2$	59.3%	176	$p = .1219^2$	64.5%	91	$p = .4395^2$
Fledging success	75.9%	71	$p = .2154^2$	70.9%	176	$p = .2287^2$	66.1%	91	$p = .0345^2$
Nest success	51.4%	71	$p = .0114^2$	42.1%	176	$p = .8681^2$	42.7%	91	$p = .0367^2$
Fall nest height	31.0cm	76	$p = .0000^1$	21.2cm	172	$p = .0000^1$	14.6cm	85	$p = .0000^1$
Nearest neighbour	71.5cm	74	$p = .1891^1$	70.5cm	172	$p = .4628^1$	71.2cm	85	$p = .6605^1$
Central: Peripheral	41: 35		$p = .6510^2$	90: 87		$p = .0000^2$	15: 72		$p = .0000^2$
New: Reused	0: 77			15: 144		$p = .0000^2$	29: 48		

[1] Significance tested with MW'U'

[2] Significance tested with Chi^2

Palmer 1962). This may be particularly true in Double-crested Cormorants where nest concealment is not a priority. The reuse of previously built structures may reduce the time and energy required of breeding birds prior to nesting (Thompson 1981). It might also be suggested that information on the previous reproductive history of a particular site may be derived from relative nest height. As nest height is strongly related to nest age (Figure 25), a courting male on a proven, taller sight might be more successful at attracting a mate than a male on an unproven new site.

As a first examination of this problem, I compared several reproductive and nest site parameters between new and reused nests (Table 14). As would be expected from the previous examination of nest height, reused nests were initiated significantly earlier than new nests. Cormorants nesting at previously used sites also laid significantly more total eggs per nest and had a significantly larger clutch size. Brood size and mean number of young fledged per nest were also larger in reused nests, but the differences were not significant.

A comparison of reproductive success between new and reused nests, however, did not reveal any significant differences or consistent patterns between these two nest types. An examination of physical nest parameters between these two groups revealed that new nests were significantly lower in height and further apart than reused nests.

A better understanding of the differences in reproductive parameters among nests of different ages can be obtained by comparing more specific nest age classes. The only exclusive age classes which I was able to construct were new nests, nests used for the second time and nests used for the third or subsequent time (Table 15).

The general trend was similar to the new/reused comparison, with reproductive output increasing with nest age. The total number of eggs laid, clutch size and number of young fledged per nest were all significantly greater in nests reused more than twice. In addition, older reused nests showed significantly greater fledging success and overall nest success than nests used for only the second time. In contrast none of the paired comparisons of reproductive output or success between new nests and nests used for the second time were significantly different.

Paired comparisons between nest site parameters revealed that new nests were lower than second use nests, which were in turn lower than older reused nests. Although

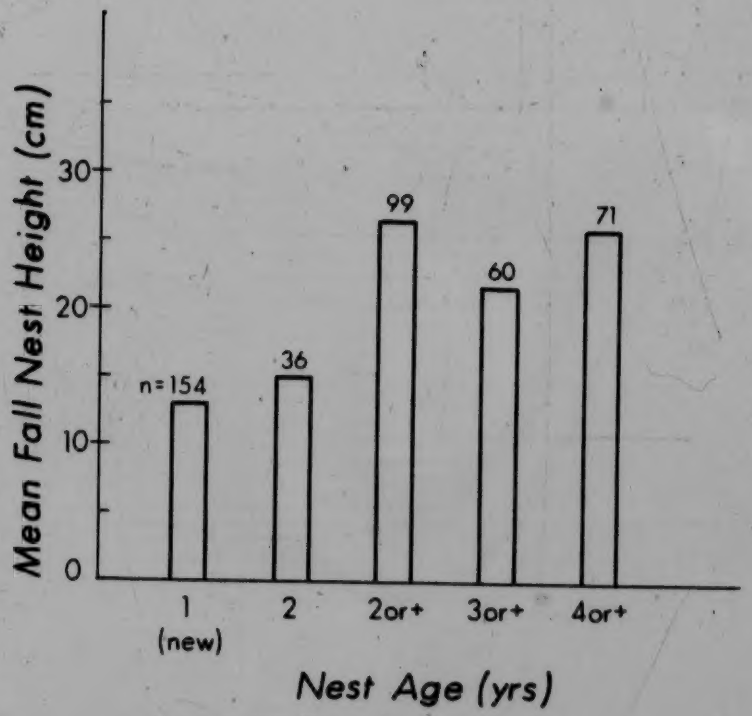

Figure 25 – Changes in nest height with nest age

Table 14: Comparison of reproductive data and nest site parameters between new and reused nests.

	New		Reused		Difference
	Mean	n =	Mean	n =	
Nest Initiation	May 17	173	May 6	281	p = .0000[1]
Total eggs	3.65	173	3.88	282	p = .0013[1]
Clutch size	3.47	173	3.65	282	p = .0185[1]
Brood size	2.19	173	2.26	281	p = .5482[1]
# Fledged per nest	1.56	173	1.66	275	p = .4191[1]
Pre-clutch success	95.1	173	94.1	275	p = .3872[2]
Hatching success	63.1	173	61.9	275	p = .6301[2]
Fledging success	71.2	173	73.5	275	p = .4453[2]
Nesting success	45.0	173	45.5	275	p = .8407[2]
Fall nest height	12.9	154	23.5	266	p = .0000[1]
Nearest Neighbour	76.5	154	70.7	264	p = .0000[1]
Central: Peripheral	30: 127		127: 146		p = 0.0000[2]

[1] Significance tested with MW'U'

[2] Significance tested with Chi^2

Table 15: Comparison of reproductive data and nest site parameters between nest age categories.

	First Use			Second Use			Third or Greater Use		
	Mean	n =	1 vs. 2	Mean	n =	2 vs. 3	Mean	n =	1 vs. 3
Nest Initiation	May 17	173	p = .0000^1	May 8	37	p = .0000^1	May 2	137	p = .0000^1
Total eggs	3.65	173	p = .5423^1	3.68	37	p = .0142^1	4.06	137	p = .0000^1
Clutch size	3.47	173	p = .9538^1	3.49	37	p = .0029^1	3.86	137	p = .0000^1
Brood size	2.19	173	p = .7196^1	2.27	37	p = .1473^1	2.65	136	p = .0034^1
# Fledged per nest	1.56	173	p = .4844^1	1.43	37	p = .0043^1	2.12	131	p = .0001^1
Pre-clutch success	95.1%	173	p = .8947^2	94.8%	37	p = .8907^2	95.1	131	p = .9907^2
Hatching success	63.1%	173	p = .6768^2	65.1%	37	p = .4352^2	68.7	131	p = .4352^2
Fledging success	71.2%	173	p = .1362^2	63.0%	37	p = .0009^2	80.0	131	p = .0062^2
Nesting success	45.0%	173	p = .4083^2	41.0%	37	p = .0047^2	54.9	131	p = .0009^2
Fall nest height	12.9cm	154	p = .0228^1	15.0cm	36	p = .0000^1	23.8cm	131	p = .0000^1
Nearest Neighbour	76.5cm	154	p = .0000^1	69.1cm	36	p = .0720^1	70.4cm	129	p = .0000^1
Central: Peripheral	30: 127		p = .0000^2	21: 15		p = .5602^2	84: 48		p = .0000^2

[1] Significance tested with MW'U'

[2] Significance tested with Chi^2

new nests were significantly further from their nearest neighbour than reused nests, the difference between the two reused categories was small and not significant. As would be expected, the mean initiation date of nests used for the third or subsequent time was significantly earlier than nests reused for the second time, and new nests were initiated significantly later than nests used for the second time.

C. Human Disturbance at the Colony Site

Although the main thrust of my research was directed at describing the annual cycle of Double-crested Cormorants in southern Alberta, whenever possible I also collected information on their reaction to disturbance. I have divided these data into two categories: a description of colony and individual responses to human disturbance, and a post hoc comparison of reproductive output and success on colonies subjected to varying levels of disturbance.

Individual and Colony Reaction to Human Disturbance

The flush distance (first and 100%) and the time to return (first and 100%) are graphed against date in figures 26 to 29 respectively. There was no clear relationship between the time of year and the distance at which the first cormorants flushed from the colony island (Figure 26). This was not unexpected, as the first birds to leave a colony were those loafing off the nests. There was little reason to believe that the attraction these birds had to the colony should vary over the breeding season.

The remaining three graphs (Figures 27-29), however, all show a similar trend. Breeding cormorants leave earlier and return later during both the beginning and end of the reproductive season.

During the height of the reproductive season, breeding birds allowed us to approach more closely before they flushed, and returned to their nests more quickly when we departed. There were, in fact, instances in which adult cormorants either returned to their nests while we were still on the island, or refused to leave until we had reached the island and approached the colony on foot (0 values on the graphs).

These data indicate that breeding cormorants were most attached to their nest sites during the peak of the breeding season, and less attached both early and late in the year. To examine this relationship, the data from each of these graphs were divided as to

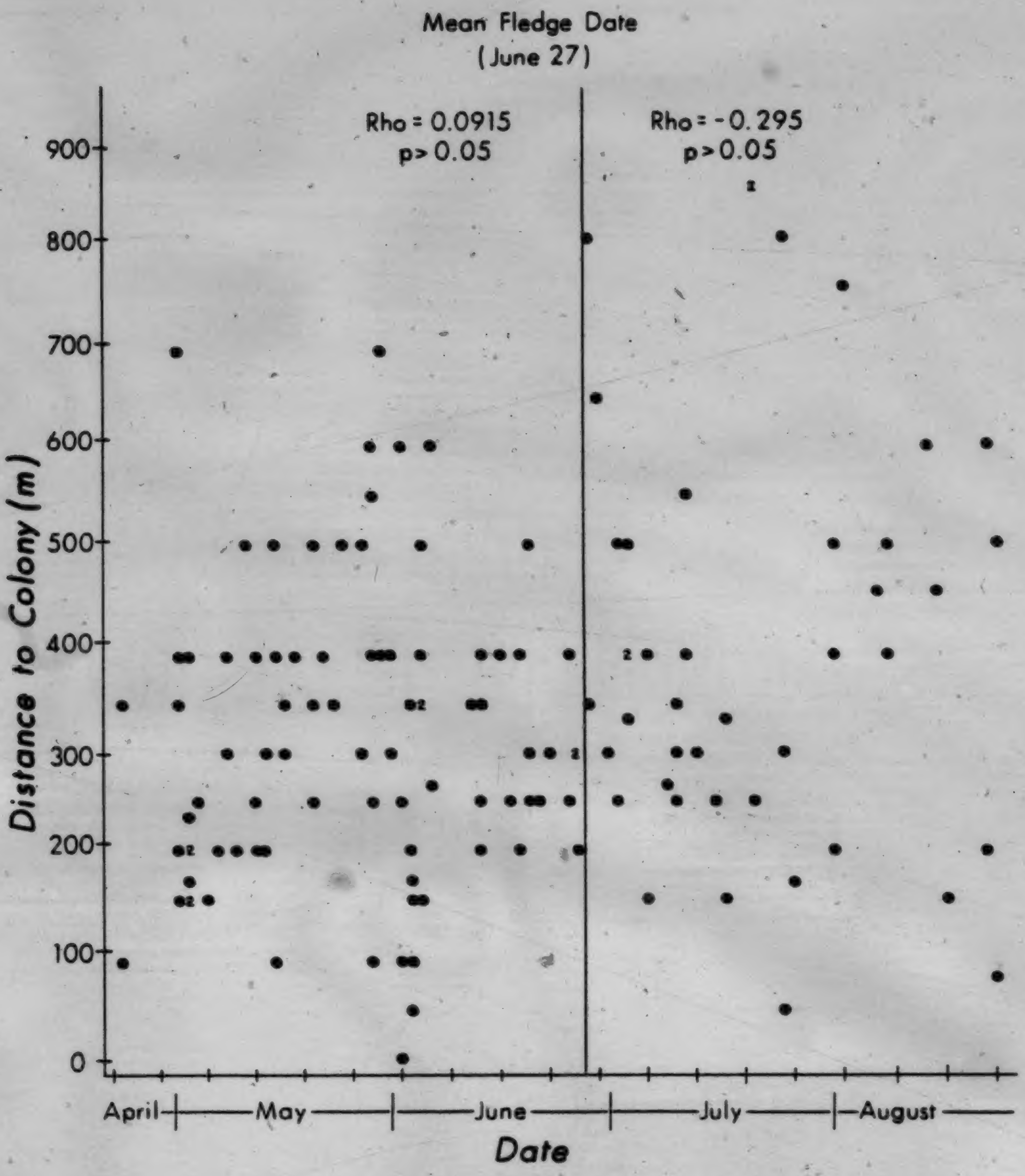

Figure 26 – Relationship between the distance at which the first cormorants flushed from a colony and date.

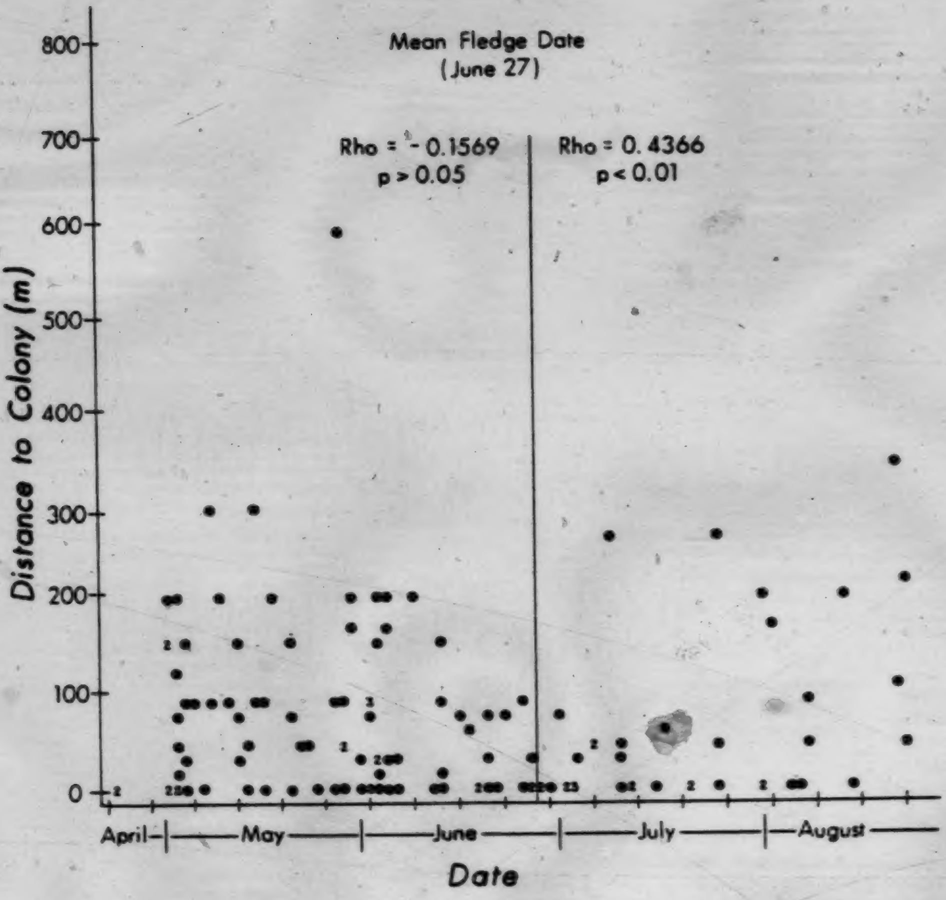

Figure 27 – Relationship between the distance at which all adult cormorants left the colony island and date.

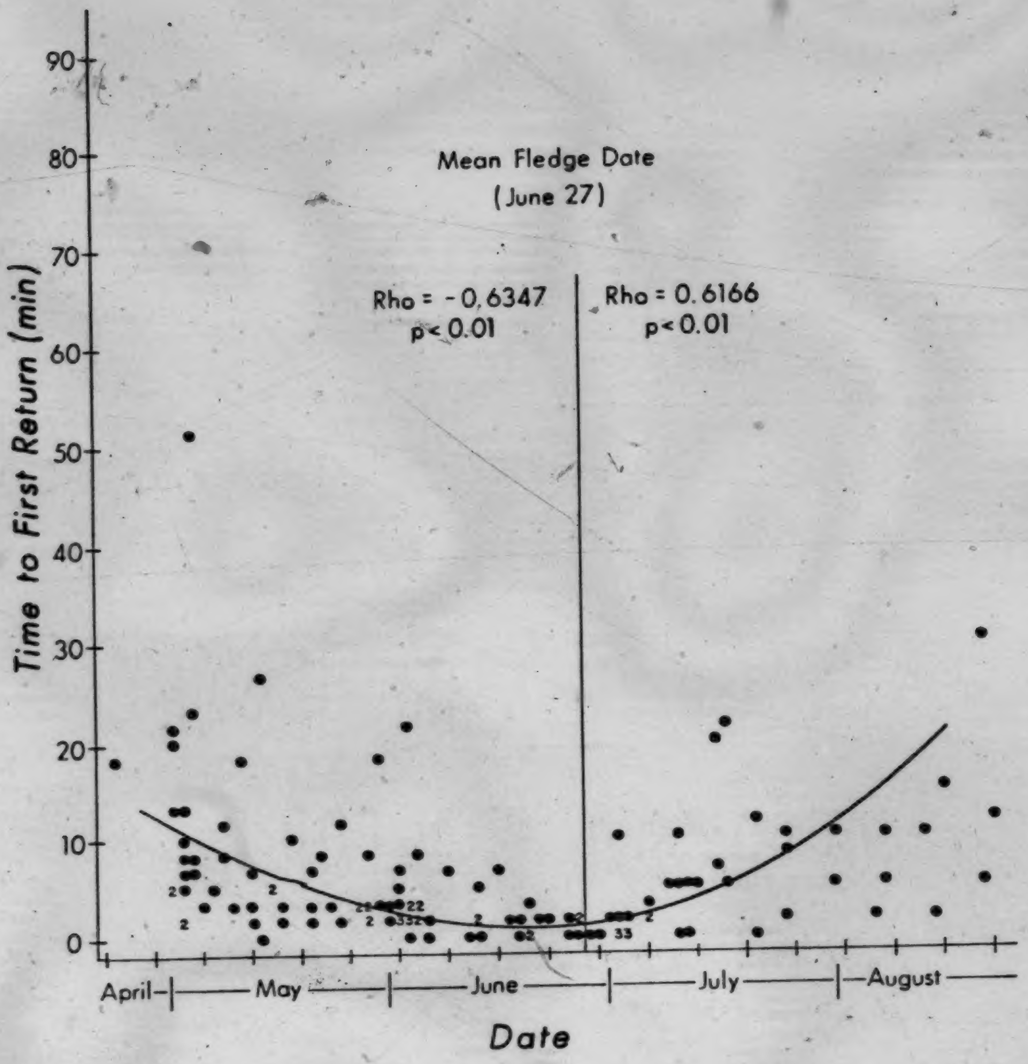

Figure 28 – Relationship between the time it took for the first adult cormorant to return to the colony island after disturbance and date. (Line hand fit to mean values)

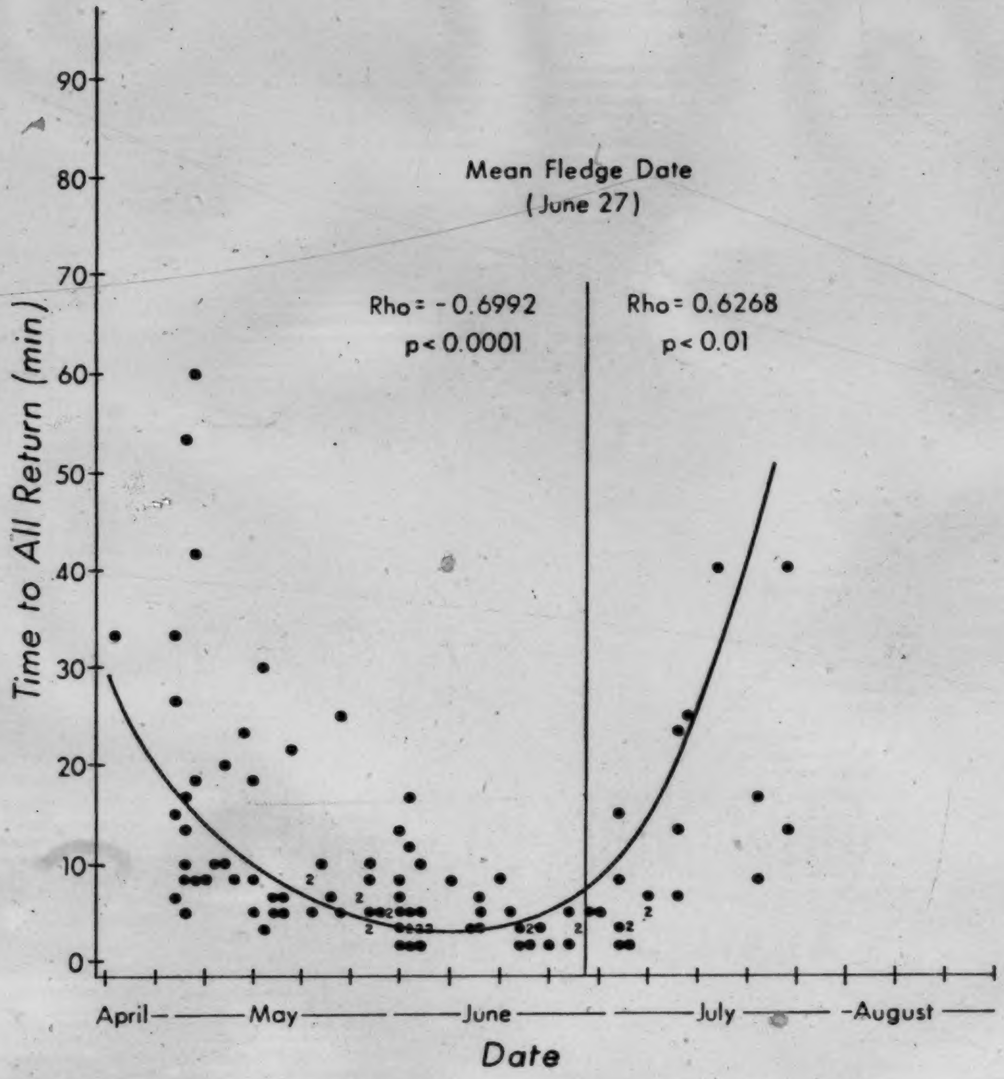

Figure 29 – Relationship between the time it took for all active nests to be occupied by an adult after disturbance and date. (Line hand fit to mean values)

being either before or after the mean fledging date of June 27. Casual observations suggested that once young were able to defend themselves and/or flee the nest in the face of disturbance, the adults were less likely to stay on their territory during a disturbance. Young generally attain these capacities during their third week of life (14-21 days), and the mean fledging date (survival to 18 days) therefore appeared to be a suitable dividing point.

All pre-fledge periods showed a significant negative correlation between date and time to return. There is a similar but positive correlation between date post-fledge and both 100% flush distance and time to return (1st and 100%) (Figures 27-29).

Using similar data, I examined the potential relationship between the amount of time we spent on a colony collecting data, and the amount of time it took for the breeding birds to return to their nests (Table 16). Within the range of times spent on the colony (7-196 minutes, mean = 57.2, SD = 36.85) the only significant relationship was a negative correlation between time on and first return. When the year was divided into the pre- and post-fledge periods, only the time to first return in the prefledge period was significantly correlated with time spent on the colony. It would appear that as the time we spent on the colony increased, the time it took the first cormorants to return to their nests decreased. There was, however, no similar relationship between time spent on the colony and the time it took for all active nests to be occupied.

An additional concept which should be addressed when considering the response of a wildlife species to disturbance is habituation. How much of the observed response, or change in response over time, is due to familiarity with the disturbance. Most colonies were studied intensively for a single year or infrequently for several years and did not provide adequate data for this type of comparison. The Lake Newell colony, however, was subjected to very similar levels of disturbance in both 1979 & 1980 and sufficient data were collected to examine this concept.

Observations of this colony suggested that these birds were, in fact, more tolerant to disturbance in 1980 than in 1979. In 21% (n = 19) of the visits in 1980, breeding cormorants remained on nests in some part of the colony during the entire data collection period. This occurred only once (6% of 17 visits) in 1979. Similarly, during all but one of the approaches to this island in 1980 (95%, n = 19), the colony was not totally

Table 16: Correlation between time spent on a colony island and time breeding birds took to return following disturbance.

	First Return	All Nests Full
Pre-fledge period	[1] $\bar{X} = 6.73$ min. ± 11.49 [2] Rho = −.3067 $p < .01$ n = 89	$\bar{X} = 9.99$ min. ± 10.83 Rho = −.1497 $p > .05$ n = 82
Post-fledge period	$\bar{X} = 5.82$ ± 6.63 Rho = −.0873 $p > .05$ n = 38	$\bar{X} = 11.83$ ± 11.49 Rho = .2234 $p > .05$ n = 18
Overall	$\bar{X} = 6.44$ ± 10.2 Rho = −.2367 $p < .01$ n = 127	$\bar{X} = 10.35$ ± 10.93 Rho = −.1553 $p > .05$ n = 100

[1] mean ± one standard deviation

[2] Spearman's Rank Order Correlation coefficient

abandoned until I had reached the shore, and often (63%) not until I approached the nests on foot. In 1979, at least some cormorants remained on their nests until I arrived in 71% of the visits (n = 17) and stayed on until I approached on foot in only 24% of the cases. Although these patterns are consistent and reinforce my personal observations, none of them attain statistical significance (Fishers Exact Test $p > .05$).

A second way I examined this phenomenon was to compare the weekly mean flush distance and time to return. If habituation was occurring, breeding cormorants should have been less willing to leave and would have returned more quickly in 1980 than in 1979. A pairwise comparison of the available data, however, revealed that although cormorants generally remained on their nests longer and returned more quickly in 1980, none of the differences in these responses attained significance (Table 17).

Throughout the study the general pattern of approach to nesting colonies was kept consistent. During 1979 and 1980, however, the rate of approach was intentionally varied to measure any potential differences in flush distance. Analysis of the flush distance response to a fast (approx. 17 km/hr) versus slow (7-9 km/hr) approach revealed no significant differences in either first or 100% flush distance during either the prefledge, postfledge or overall periods. This lack of apparent difference may, however, be due to the relatively narrow range in approach speed. Observations of non-research disturbance showed that it was possible for a silent boat to drift slowly onto the colony island without causing any nests to be abandoned. Conversely, a high powered speed boat more than 1 km away was observed to cause a panic flight including the brief abandonment of some nests.

Reproductive Consequences of Human Disturbance

In addressing the reproductive consequences of human disturbance on colonial bird nesting islands, the question to ask is not whether human visitation can affect reproduction but rather how does a particular level of disturbance influence reproductive success. It is relatively simple to eliminate or reduce the annual reproductive output of a colony, but is it also possible to visit a colony island without significant reproductive disruption?

During the three years of this study, every effort was made to minimize the influence of our visits on the reproductive output of the colonies studied. In general,

Table 17: Comparison of the response of cormorants to research disturbance in 1979 and 1980: Lake Newell

	Weekly Mean Values			
	1979[1]	1980[2]	n =	Difference
First Flush (m)	405.4	457.7	14	$p > .05$
All Flush (m)	39.5	26.9	13	$p > .05$
First Return (min.)	2.78	1.48	13	$p > .05$
All Return (min.)	5.93	5.18	9	$p > .05$

[1] Comparison of weekly mean values in cases where data was available in both 1979 and 1980.

[2] Significance tested with Wilkoxen paired sample test.

colonies were not visited in the heat of the day or during particularly cold or wet weather. Young were normally prevented from escaping to the water until at least 4 weeks of age, and large creches of young were not allowed to develop and/or stay in one place. Late hatching very small young which were exposed to high temperatures or intense sun during banding operations were covered with fresh green vegetation pulled up from the colony margin to provide shade.

I collected two levels of data which may be applied to this problem. Detailed reproductive information, collected during one or two visits per week to the Hays, Newell and Tilley South colonies in 1980 and the Newell and Tilley North colonies in 1979, provided the primary data on 'disturbed' colonies. In years when they were not intensively studied, these, and a variety of other colonies in southern Alberta, were visited two or three times in a year to collect reproductive information in a relatively undisturbed setting. 'Undisturbed' colonies were normally visited once in the first week of May and June, and in mid-July to document nest initiation, clutch size, and number of late season young, respectively. Similarly timed single day counts were extracted from the frequently disturbed colonies for comparison.

With the above data, it was possible to compare detailed reproductive parameters from colonies subjected to two levels of intensive research disturbance (once vs. twice per week). It was also possible to compare these 'disturbed' colonies with relatively undisturbed colonies visited only once or twice prior to the data collection visit.

Intensive Disturbance

The Newell 1979, Newell 1980, and Hays 1980 colonies were visted once per week throughout the reproductive season, and the Tilley North 1979 and Tilley South 1980 colonies were visited twice per week to collect detailed reproductive information. Although a comparison of these colonies may suggest differing effects of these two disturbance levels, it should also be noted that the less disturbed islands all supported older and larger colonies while the more disturbed Tilley colonies were both newer and smaller. As there were no formal control colonies, it is not entirely possible to separate the effects of disturbance from the differing reproductive output of old and large versus new and small colonies.

A comparison of these two disturbance types revealed that all categories of reproductive output were significantly greater in the colonies visited twice per week (Table 18). This difference may, however, stem from some inherent difference in the cormorants occupying the more disturbed colonies, or the quality of nesting habitat; factors not directly influenced by disturbance.

A more precise measure of how disturbance influenced the ability of cormorants to nest and raise young was the comparative success of raising eggs to hatching and nestlings to fledging (Table 18). Although all categories of reproductive success were higher in colonies visited twice per week, the differences were small and only fledging success approached statistical significance ($p = .0512$).

A second approach to this problem is to compare the relative abundance of nests which failed and/or were abandoned between colonies visited once or twice per week. If the harrassment caused by disturbance forces some age or experience classes of cormorants to abandon their nests, empty nests should be more common in more disturbed colonies. I found, just the opposite to be true. Colonies visited once per week had significantly more nests which fledged no young than those visited twice per week (33% vs. 23%, Chi^2 $p = 0.0168$).

Disturbed vs. "Undisturbed" Colonies

A second estimate of the reproductive consequences of disturbance was obtained by comparing colonies which were intensively studied with those which were visited only 2 or 3 times per year. Equivalent 'single visit' data was available to compare mean clutch size and number of late season young per active nest between 4 disturbed and 18 'undisturbed' colony specific reproductive seasons (Table 19). An overall comparison of these values revealed no significant difference in the number of late season young between the two disturbance levels (MW'U' $p > .10$). Overall clutch size, however, was significantly larger in disturbed colonies (MW'U' $p = .01$).

Once again, a better measure of the effects of disturbance may be gained by comparing the relative ability of cormorants to produce young from eggs laid. When all data were compared, nest success (clutch size divided by number of late season young per nest) was higher in undisturbed colonies (44.6% vs. 49.3%, Chi^2 $p = .0001$).

Table 18: Comparison of reproductive data between colonies visited once or twice per week.

	Once Per Week		Twice Per Week		
	Mean	n =	Mean	n =	Difference
Total eggs	3.62	303	3.99	186	$p = .0000^1$
Clutch size	3.38	303	3.78	186	$p = .0000^1$
Brood size	2.07	303	2.33	186	$p = .0280^1$
# Fledged per nest	1.46	303	1.77	186	$p = .0056^1$
Pre-clutch success	93.4%	303	94.7%	186	$p > .05^2$
Hatching success	61.2%	303	61.6%	186	$p > .05^2$
Fledging success	70.5%	303	76.0%	186	$p = .05^2$
Nesting success	43.2%	303	46.8%	186	$p > .05^2$

[1] Significance tested with MW'U'

[2] Significance tested with Chi^2

Table 19: Mean clutch size and number of late season young per nest as determined by single counts of disturbed and 'undisturbed' colonies.

Disturbed Colonies	Mean Clutch Size	Mean Late Season Young	[1]n =
Newell 1980	3.33	1.57	732
Tilley North 1979	3.74	1.79	58
Tilley South 1980	3.65	2.20	122
Hays 1980	3.43	1.09	314
Disturbed Total	3.41[2]	1.52[2]	1226
Undisturbed Colonies			
Newell 1978	2.89	1.53[3]	525
Tilley North 1978	3.04	1.49	46
Tilley South 1978	3.04	0.96	23
Tilley South 1979	1.44	1.91	9
Hays 1979	3.24	1.23	314
Murray Lake 1978	3.00	1.34	3
Murray Lake 1980	3.61	1.00	23
St. Mary's Reservoir 1978	2.72	1.45	29
St. Mary's Reservoir 1979	3.64	1.29	39
Keho Lake 1979	2.60	1.29	5
Lake Newell - Small Outlying Colony 1980	2.75	1.66	4
Barkhausen Lake 1978	2.63	1.43	16
Barkhausen Lake 1979	2.06	2.04	16
Barkhausen Lake 1980	3.59	2.43	44
Little Bow Reservoir 1978	3.13	1.52	38
Little Bow Reservoir 1980	3.20	1.26	10
Dowling Lake 1978	2.94	1.86	18
Dowling Lake 1979	2.60	1.60	5
Undisturbed Total	3.00[2]	1.48[2]	1167

[1] Total number of active nests

[2] Weighted mean

[3] Estimated from number of 18+ day old young in 38 marked nests

A similar comparison between years when the Newell, Tilley N, Tilley S and Hays colonies were disturbed or 'undisturbed' revealed a similar trend towards higher nesting success in undisturbed years (44.6% vs. 47.0%, Chi^2 p = .0457). It would appear that 'undisturbed' colonies produced more young per egg laid than disturbed colonies. Within disturbed colonies sample size was too small for meaningful statistical analysis between different intensities of disturbance. Both clutch size and number of late season young per nest, however, were greater in intensively disturbed colony years (1 visit per week: Clutch = 3.36, late season young = 1.46, 2 visits per week: Clutch = 3.68, late season young = 2.07).

At least one factor limited the reliability of this analysis. In 1980 over one-third (231) of the young cormorants on the Hays colony died between June 26 and June 30. The cause of this mortality could not be determined with certainty, but malicious human disturbance is suggested. If these 231 dead young are included as late season young for the Hays 1980 colony, the apparent difference between nesting success on these four colonies in disturbed vs. 'undisturbed' years reverses, with significantly more young raised per egg laid in intensively studied years than in relatively undisturbed years (50.1% vs. 47.0%, Chi^2 p = .0118).

It would appear that research disturbance alone did not cause a decrease in nesting success within colonies, between years. If, however, the effects of an uncontrolled non-research disturbance are included, then disturbed colonies were less successful than the same colonies in relatively undisturbed years.

V. Discussion

In the following section I will summarize and integrate the data presented in the following manner. In order to understand if and how much the reproductive data have been affected by the research method, I will first examine the response to and effects of research disturbance. The remainder of this section will be made up of an examination of how reproductive values vary between several colony and nest site parameters. Most important among these variables will be: year, colony age and size, nest and colony initiation date, nest placement and nest age.

A. Double-crested Cormorant Response to Research Disturbance

In ecological research a primary paradox often must be dealt with: while collecting data on a system the effects of the researcher on the system being studied must be evaluated. It is usually difficult to separate the data which result from the observer's influence from those which describe the system in it's natural condition. This problem is particularly acute in studies of colonial birds, where large numbers of nests, eggs, young or adults are influenced by a single visit to, or even near, a colony island, and where the ability to control this disturbance while collecting data is limited. It is essential, however, when attempting to describe or compare the reproductive output or success of a species, to estimate the impact of the data collection technique on the results obtained. It is equally important, when making management decisions, to understand and be able to predict the response of a species to disturbance, and the effect that various levels of disturbance have on the ultimate reproductive output.

While it was not possible to evaluate non-research disturbance in this study, observations during 1979 and 1980 suggest that the intensively studied colonies were not frequently disturbed by non-research visitation. The single major exception however, caused an unprecedented mortality at the Hays colony in 1980. Fortunately, this disturbance occurred late enough in the season (Approximately July 1) that most measures of reproductive success were not greatly affected. The fact that what I believe to be vandalism could cause the death of more than one-third of the young produced by a large colony in less than four days, however, is sufficient evidence that uncontrolled human disturbance can, and sometimes does, have profound reproductive consequences.

To a large extent, the impact of any disturbance on a nesting colony is dependent on the response it elicits from the breeding adults. Although the basic response of fleeing the colony island remains the same, the pattern of adult cormorant response changes in a predictable fashion over the reproductive season. Early in the year when pairs and nests are being established, cormorants are very wary of human disturbance. They flush from their nests more readily and are significantly slower to return after a disturbance (Figures 26-29). Their reaction to disturbance decreases over the season, reaching a minimum at about the time when most young have attained three weeks of age. After this time, adults again become increasingly wary of human visitors.

Contrary to observations in Quebec reported by Ellison & Cleary (1978) Double-crested Cormorants in Alberta never actively defended their nests from human visitation. In a relatively long lived bird such as a cormorant, the basic flight response to a possibly lethal disturbance is a reasonable strategy. It is probably more beneficial to abandon a particular clutch or brood than to aggressively defend them and possibly not live to either renest or breed again in subsequent years. Within this limit, however, cormorants appear to pattern their behavior in response to the needs of their eggs and young.

I would suggest the following rationale for the patterns observed. Early in the season when laying has just begun, eggs are both thermally more tolerant and easily replaced by additional laying. At this time there would be less value in protecting a nest site against either human disturbance or the associated gull predation and/or thermal stress which accompanies it. As incubation and embryonic development begin, eggs become increasingly vulnerable to heat stress (Romanoff 1960). At this point, replacing lost eggs would increase in both metabolic and time costs and would require a physiological 'restart' by the female. Considering the relatively truncated breeding season available to cormorants in southern Alberta, there may not be time for a breeding pair to relay and successfully raise a brood to independence. There is, therefore, an increasing value to the adult cormorant to protect it's eggs as the season progresses.

At hatching, the thermal tolerance of chicks is very low and newly hatched young are functionally cold-blooded (Dunn 1976). Just a few minutes exposure to high temperatures and direct intense sunlight can cause death during the first week of age

(McLeod and Bondar 1953, W. Van Schick pers. comm.). During the late incubation and early brood periods, the predation pressure applied by gulls from their adjacent colonies may also be reaching a peak, as gull chicks have hatched and the food requirements of gull breeding pairs have increased accordingly. It is during this early post-hatch period that cormorant reproductive output is most at risk. It is also during this period that adult cormorants are most attached to their nests. They are hesitant to leave them undefended and return rapidly following a disturbance.

After the young cormorants reach three weeks of age they are both behaviorally and metabolically able to control their body temperature. At this age they are also able to defend themselves against attack by gulls. In fact, as the season progresses, gulls will abandon the colony island and move their family groups elsewhere, reducing but not eliminating their predation pressure. From this post-fledge period to the end of the season, adult cormorants become increasingly less attached to the colony. Eventually they abandon the nest site, and return to the colony only to feed their young, loaf, and roost at night. Both their flush distance and return rate increase to early season levels. By early August, in fact, many adults may not return to their colony after a disturbance but will remain on another island or point to roost.

In order to combine the data collected in all years of this study in an equal manner, it is necessary to show that no significant variation in reproductive parameters resulted from adult habituation to the research method. During 1979 and 1980 the Newell colony received identical treatment, and if habituation were to occur, it would be most visible on this colony. A comparison of all measures of adult response to disturbance at this colony between these two years revealed no significant differences (Table 17). Although a trend toward increased tolerance in 1980 was noted, a similar comparison of the frequency of adults remaining on or returning to their nests while a researcher was on the colony revealed no significant differences between 1980 and 1979. It appears safe to assume that the behavior of adult cormorants on the Newell colony did not differ significantly between 1979 and 1980, and that habituation, if it did occur, did not have a significant impact on any of my study colonies.

B. The Reproductive Consequences of Research Disturbance

It is not possible to visit an active cormorant colony without having some impact on the breeding birds. Often this impact is limited to a brief and probably ineffectual interruption of incubation. On occasion, however, our research visits caused direct mortality by facilitating gull predation of eggs and/or young, by causing thermal stress of newly hatched chicks, or by allowing the suffocation of small young in the large creches of young which often form in response to disturbance. In the absence of human disturbance on or near the colony, these types of mortality were either never, or very infrequently observed. In over 575 hours of colony observation from adjacent blinds, no predation of eggs or young was observed except that associated with human disturbance.

When data from all colonies and years were compared, 'undisturbed' colonies were significantly more successful at converting clutches into late season young. The actual number of late season young per nest, however, did not differ significantly between disturbance types. As this comparison relied on data from a broad variety of colonies and years, it was difficult to determine how much of the observed variability was due to different levels of disturbance and how much was due to other colony or year variables.

It was not possible to reverse disturbance levels between colonies and years to control for this variability. A paired comparison of four colonies which were intensively disturbed in one year and relatively undisturbed in a previous year revealed a significant decrease in nesting success in intensively disturbed years. Further analysis revealed that this difference, favoring reproductive success in undisturbed years, was reversed if the effects of a single known non-research disturbance (at Hays 1980) was excluded.

When two levels of intensive research disturbance were compared, there was no significant difference in the ability of breeding cormorants to convert clutches to broods or fledge young from broods. In fact, the small differences which did occur, favored the more frequently disturbed colonies.

Two general conclusions can be drawn from these data. First, it appears that while intensively studied colonies are less successful than relatively undisturbed colonies at converting clutches to late season young, much of this difference may stem from variations in factors other than relative research disturbance. Second, there appears to be no significant or consistent difference in reproductive success between colonies visited once versus twice per week. These data suggest that while the overall reproductive parameters used in this study may slightly underestimate reproductive output and success for southern Alberta cormorants, the data from colonies visited once vs. twice per week were not differentially affected by research disturbance.

C. Seasonal Variation in Reproductive Parameters

When data from all colonies and years was pooled, there was a consistent and significant decrease in all reproductive output measures as the season progressed (Figure 8). With the exception of pre-clutch success, there was a similar negative correlation between nest initiation date and all measures of reproductive success (Figure 9).

This general pattern of decrease in one or more reproductive parameters as the season progresses has been noted in many species (Ryder 1975 in Ring-billed Gulls, Hogan 1979 in Great Cormorants (*P. carbo*), Snow 1960 in Shags (*P. aristotelis*), Coulson and White 1958 in Kittiwakes (*Rissa tridactyla*), Parsons 1975 in Herring Gulls (*Larus argentatus*)). Although studies involving known aged individuals are rare, the most common explanation of this pattern is that younger, less experienced birds tend to breed later in the season, and their lower reproductive output and/or success tend to decrease the mean reproductive success or output of later nests.

Ryder (1980) provides a thorough review of the influence of age on the breeding biology of colonial seabirds. He summarizes the available data from research on known aged populations by stating that older, established pairs arrive earlier at the breeding colony and lay larger clutches and eggs that, on average, produce more fledged young per season than do younger pairs or pairs nesting for the first time.

In cormorants, Hogan (1979) found that younger *P. carbo* nested later in the season, during the period when mean clutch size and hatching success was low. As he could not document the clutch size of known aged individuals, the observed relationship is only suggestive. Van de Veen (1973) reported that 2 year old *P. auritus albociliatus* on the Pacific coast produced smaller numbers of young per nest than mature (3+) breeders (1.5 vs. 2.0, n = 4, 60+). He did not, however, record nest initiation dates and seasonal variations could not be calculated. Snow (1960) attributed the lower breeding success of *P. aristotelis* late in the season to the fact that most late nests were new nests occupied by young birds. Using data from known aged *P. aristotelis*, Potts (1966, cited in Hogan 1979) found progressively earlier nesting dates with increased age, with early nesting birds occupying the best nest sites available.

The extent to which reduced age and breeding experience influenced late season nests in this study is unknown. Although the earliest cormorants with immature plumage returned several days later than the earliest adults, both age classes appeared to increase at a similar rate, reaching maximum levels in early June. This similarity in the date of return, however, does not necessarily indicate that breeding occurs at the same time. Ryder (1975) found that pairs of Ring-billed Gulls with at least one member in immature plumage nested later even though they arrived on the colony at the same time as mature pairs.

At the Newell colony in 1980, 2 marked nests were occupied by pairs with at least one 2 year old cormorant, presumably a first year breeder. These 2 nests were initiated on May 18. This was 9 days after the mean initiation date for that colony year, but was within one standard deviation of the mean and should not be considered overly late. These 2 breeding pairs laid 2 eggs each, hatched an average of 1.5 eggs per nest (75% hatching success) and fledged at least 2 young (67% fledging success). Although their clutch size was considerably smaller than the Newell 1980 mean of 3.6, the 50% nesting success was very similar to the colony average of 48% for that season. From this very small sample, it would appear that younger Double-crested Cormorants on established colonies may have lower reproductive output (clutch and brood size) but they are not less successful at fledging young per egg laid than the colony average.

A second mechanism which is often invoked to explain seasonal declines in reproductive success suggests that late nesting (younger?) birds are often relegated to less desirable breeding habitat (Hogan 1979, Ryder 80, Blus and Keahey 1978, Tenaza 1971). Southern Alberta colony islands, however, are relatively homogeneous and potential reproductive habitat is not obviously limited. Birds that nest early do, however, preferentially select previously used nest sites, forcing pairs that establish later onto previously unused sites. Palmer (1962) and Thompson (1981) have both suggested that reused nests may be prepared for laying several days more quickly than previously unused sites. This, in itself, would explain some of the difference in mean initiation date between nest types. The reuse of a previously built nest, however, may also provide a reproductive advantage by decreasing the energy a pair devotes to nest construction, thus increasing the time and energy available for courtship, egg production and laying. The relatively small but significant difference in clutch size associated with reused nests tends to support this proposition (Table 14). There was, however, no significant difference in reproductive success between new and reused nest types. If an advantage was gained by reusing a nest, the benefit was apparently limited to a slight increase in the energy available for egg production.

Several previous authors have also suggested that breeders that return later are forced into peripheral nest sites which are less desirable than central locations. Cormorants in Alberta clearly preferred central locations, establishing nests at these sites significantly earlier than at peripheral locations (Table 11). It is not surprising, then, that the number of young fledged per nest was significantly greater in central nests. If early (older) birds select central sites, and are more productive, then central nests should also be more productive. Nest success was also significantly greater in central nests. Once clutches were complete, pairs nesting at central sites were more successful at fledging young than were those at peripheral sites.

Although these data suggest that central nests may provide some reproductive advantage, it is difficult to discover whether this is due to variations in timing or habitat value. When the year was divided into early and late periods and early peripheral nests were compared with late central ones, the data suggested that any potential difference in habitat value was overpowered by the impact of variations in timing (Table 12).

From the above analysis, I suggest that while variations in habitat utilized by breeding cormorants have some impact on reproductive output and success, they can not adequately explain the observed seasonal decline in all reproductive parameters. A study of this population, involving known-aged individuals and more sensitive measures of habitat quality will be necessary before the reasons behind this seasonal decline can be documented.

D. Annual Variation In Reproductive Parameters

Table 20 provides a summary and comparison of reproductive parameters measured in 1979 and 1980. All measures of reproductive output and all reproductive success parameters except fledging success were significantly greater in 1980. The relative stability of fledging success seems to indicate that the majority of the observed annual variation revolves around the ability of cormorants to lay and hatch eggs.

Several authors have recorded annual variations in pre-fledging parameters (Mitchell 1977, Hogan 1979). Van Tets (1959) noted a 20% increase between 1958 and 1959 in the total number of eggs laid per nest in Double-crested Cormorants on the Pacific Coast of B.C. The majority of this difference was a result of differential predation followed by relaying, and both brood size and fledging success remained remarkably stable over the years studied. Although predation in my study was significantly more frequent in 1979, the number of eggs lost was relatively small. If, however, a significant proportion of the 39% of eggs which disappeared were lost to predators, this single factor may have been responsible for much of the difference in hatching success between 1979 and 1980.

If, as I have suggested, predation only occurs in association with human disturbance, and predation was greater in 1979 than 1980, then human disturbance must have been more frequent or more disruptive in 1979. The frequency of and response to my research disturbance, however, was similar between years. The additional disturbance, if it occurred, must have resulted from other visitations in 1979.

Although I do not have firm data to support this proposition, more non-research disturbance of colonies may have occurred in 1979. The new small colony studied in 1979 was located on the Tilley North reservoir (Figure 2). This reservoir supports a sport fishery of whitefish (*Coregonus clupeaformis*) and northern pike (*Esox lucius*) and is frequented by many more fishermen than the adjacent Tilley South reservoir which was studied in 1980. In fact, a combination of flooding caused by increased reservoir storage and disturbance by fishermen combined to cause the failure and abandonment of this colony prior to hatching in 1980. Although the known loss to predation at Tilley North in 1979 was not particularly high (4.5%), many eggs disappeared from nests (36%), possibly reflecting a high level of non-research disturbance. At the relatively undisturbed Tilley

Table 20: Summary of comparisons of reproductive data and individual egg fates between 1979 and 1980.

		1979		1980		Difference
		Mean	n =	Mean	n =	
Nest initiation		May 13	163	May 9	332	p = .0000[1]
Total eggs		3.60	163	3.84	333	p = .0012[1]
Clutch size		3.23	163	3.67	333	p = .0000[1]
Brood size		1.53	163	2.47	332	p = .0000[1]
# Fledged per nest		1.11	163	1.82	326	p = .0000[1]
Pre-clutch success		89.7%	163	95.6%	326	p = .0000[2]
Hatching success		47.4%	163	67.3%	326	p = .0000[2]
Fledging success		72.6%	163	73.7%	326	p = .7611[2]
Nesting success		34.4%	163	49.6%	326	p = .0000[2]
Egg Fate:	Hatched	42.1%	225	65.2%	727	p = .0000[2]
	Preyed upon	5.1%	27	4.0%	45	p = .0259[2,3]
	Kicked	3.2%	17	4.9%	55	p = .5947[2,3]
	Crushed	0.9%	5	1.3%	15	p = .8949[2,3]
	Infertile or Addled	9.7%	52	6.5%	72	p = .0000[2,3]
	Disappeared	39.0%	208	18.0%	201	p = .0000[2]

[1] Significance tested with MW'U'

[2] Significance tested with Chi^2

[3] Disappeared category excluded in calculation of significance

South in 1980, known predation was, in fact, higher (6.6%), but egg disappearance was much lower (14.5%). Although annual variations in other factors may have influenced these figures, I suspect that disturbance by fishermen was at least partially responsible for the higher losses in 1979.

A similar scenario can be developed for differential non-research disturbance at the Newell colony between 1979 and 1980. In May of 1979, the Alberta Fish and Wildlife Division placed a floating tire breakwater around the north and west ends of this colony (Anderson 1982) anchoring it approximately 200 m. from the island. The placement and repair of this breakwater required several (6-7) days of intensive effort by work crews on and near the island, and resulted in disturbance with known gull predation of eggs and young cormorant chicks during the incubation and hatching periods. In 1980 the placement of the breakwater was considerably more efficient and minimal maintainance was required during the reproductive season. This disturbance was therefore less frequent, less intensive and provided fewer opportunities for predation in 1980.

In addition to this official disturbance, my observations at Lake Newell suggest that this colony may have been visited more frequently by pleasure boats in 1979. This lake supports a provincial park, and although access on or within 1/2 mile of the colony has been prohibited since 1977, marker buoys defining the 1/2 mile limit were not placed until mid-May of 1979. Once in place, these buoys were generally respected, but several unauthorized boats were observed near enough to the colony to flush breeding birds before and shortly after the buoys were initially placed in position. Although the reproductive impact of these visits was probably slight, more disturbance was observed in 1979 than in 1980.

The observed annual trend in reproductive success and egg loss at the Newell colony may reflect these differences in the frequency of non-research disturbance. The frequency of predation and disappearance were both significantly higher in 1979 (predation = 5.5% vs. 1.8% Chi^2 $p = 0.0027$; disappearance = 41.6% vs. 24.7% Chi^2 $p = 0.0000$). While these differences do not explain variations in clutch size, they do undoubtedly contribute to the lower reproductive success observed in 1979.

A second variable which may have contributed to lower reproductive output and success was the cool spring weather in 1979 (Figure 4). The temperatures that breeding cormorants were exposed to between their return and the mean nest initiation date were, on average, 8.4°C cooler in 1979 vs. 1980. During this period in 1979, the minimum daily temperature was at or below freezing 81% of the time, as compared with 14% of the time in 1980.

There are at least two ways in which cooler temperatures may have reduced breeding success in 1979. Eggs laid early in the season but not closely incubated may have suffered from exposure to freezing conditions. This may have resulted in the significantly higher rate of infertile or addled eggs present in 1979 (Table 20). Cormorant eggs, however, appear to be very tolerant to low temperature stress, remaining viable after being cooled to an internal temperature of 0.5°C (W. Van Scheik pers. comm.).

A second mechanism by which cool spring temperatures may have effected a reduction in reproductive output, and possibly success, is by delaying the initiation of breeding. Many north temperature zone birds have been found to breed later in cool, late springs as opposed to warm, early ones (Immelmann 1971). Such a relationship was found in Alberta cormorants, with the mean nest initiation date being more than 4 days later in the cool spring of 1979.

This delay in nest initiation may reduce reproductive output in several ways. Lake ice cover associated with cool spring temperatures, may have reduced the availability of food and feeding areas for breeding birds. Laying begins shortly (5 to 14 days) after cormorants return to southern Alberta from wintering grounds 4 to 6,000 km away, and early spring feeding conditions may be critical for the replenishment of food reserves used in migration. If feeding is prevented or nutritional reserves are expended while waiting for suitable feeding areas to become ice free, breeding birds may be nutritionally stressed. Limited nutrient intake may, in turn, decrease the number, size or hatchability of eggs produced (Scott 1973), and may have contributed to the poor reproductive performance observed in the first nesting week of 1979 (Figure 8).

Even if nutrition was not limited, a delay in overall nest initiation may have reduced reproductive output. As was documented in the previous section, clutch size is negatively correlated with nest initiation date (Figure 8), and by preventing early nesting, the frequency of the most productive clutch sizes may have been reduced.

E. Nest Site Selection: Spatial Variation in Reproduction

When a mature cormorant returns to southern Alberta in the spring, it has a wide variety of potential nest sites from which to choose. The ultimate site chosen will reflect nesting habitat preferences. If these preferences are based on differential reproductive suitability of a site, then the first sites chosen may be expected to be more productive and/or successful than later occupied and possibly less suitable habitat. I examined these habitat preferences and associated reproductive variability at two levels: breeding colony selection and individual nest site selection.

Colony Site Selection

Between the two colony types studied, cormorants returned and bred first at old, large colony sites. Mitchell (1977) found a similar relationship in Utah and suggested that more intense competition for limited nest sites may encourage birds breeding at larger colonies to return early and therefore be assured of a prime nest site. Similarly, Coulson and White (1960) found that Kittiwakes returned earliest to larger, high density colonies where sites may be more difficult to obtain. Although space per se is not limited on most Alberta colony islands, prime (reused) nest sites are limited and nest site competition may be a factor influencing the earlier return to large colonies.

If the earlier initiation of old, large colonies reflects habitat preferences based on reproductive suitability then one would expect old, large colonies to have greater reproductive output and success than new, small colonies. I found just the opposite to be true (Table 21). All measures of output were significantly greater at new colonies. Differences in reproductive success, while not significant, also favored the new, small colony type. Although these differences are relatively small (< 0.4 eggs or young, < 5.5% success) their consistency suggests that new, small colonies have some reproductive advantage over old, large colonies.

This relationship is contrary to the findings of several other workers. Van de Veen (1973) found that the newest Double-crested Cormorant colony had the lowest clutch size and production. He attributed this to decreased clutch size of younger parents who were more common in this new colony. Coulson and White (1960) found that long

Table 21: Summary of comparisons of reproductive data and individual egg fates between colony types.

		Old and Large Colonies		New and Small Colonies		Difference
		Mean	n =	Mean	n =	
Nest initiation		May 9	309	May 13	186	p = .0000[1]
Total eggs		3.62	310	3.99	186	p = .0000[1]
Clutch size		3.38	310	3.78	186	p = .0000[1]
Brood size		2.07	309	2.33	186	p = .0280[1]
# Fledged per nest		1.46	303	1.77	186	p = .0056[1]
Pre-clutch success		93.4%	303	94.7%	186	p = .2261[2]
Hatching success		61.2%	303	61.6%	186	p = .8672[2]
Fledging success		70.5%	303	76.0%	186	p = .0512[2]
Nesting success		43.2%	303	46.8%	186	p = .1367[2]
Egg Fate:	Hatched	56%	536	59%	416	p = .1697[2]
	Preyed upon	3.3%	31	5.9%	41	p = .0213[2,3]
	Kicked	5.4%	51	3.0%	21	p = .0096[2,3]
	Crushed	0.7%	7	1.9%	13	p = .0549[2,3]
	Infertile or Addled	7.5%	71	7.6%	53	p = .7812[2,3]
	Disappeared	26.9%	256	21.9%	153	p = .0218[2]

[1] Significance calculated with MW'U'

[2] Significance calculated with Chi^2

[3] Disappearance category excluded in calculation of significance

established Kittiwake colonies had fewer young (inexperienced) breeders than young colonies. In a later paper, Coulson (1966) reported that clutch size and breeding success were lower in younger and less experienced pairs. From this I assume younger colonies of Kittiwakes would also show lower output and success than older colonies. Unfortunately, I do not have adequate data to determine the relative age composition of my colony types. Although nest initiation was later on new, small colonies, my observations suggest that this does not reflect a differential abundance of (young) less successful breeders.

One explanation which may contribute to the better performance of new, small colonies is the fact that they were more synchronous than old, large ones (Figure 13). Darling (1938) was first to suggest that increased synchrony resulted in greater reproductive output. He proposed that large colonies would experience greater social stimulation leading to more synchronous laying. A high proportion of young would therefore hatch in a short period, reducing the probability of predation on each individual chick. Many authors have subsequently studied aspects of this relationship with conflicting results (see Gochfeld 1980 for a review).

The data from my colonies both support and conflict with Darling's hypothesis. Large colonies, are in fact, less synchronous than smaller ones in the same region. The spread of laying was greater in large colonies in both 1979 and 1980. If social stimulation mediates reproductive synchrony then it would appear that the pairs breeding in the smaller colonies receive more social stimulation, rather than less as suggested by Darling (1938).

These smaller more synchronous colonies do, however, produce more young per nest than the older less synchronous ones. Although much of this difference stems from larger mean clutch size, pairs breeding on small colonies are also numerically more successful at fledging young. Although these differences may reflect the benefits of reproductive synchrony, the potential influence of disturbance must also be considered.

As previously mentioned, new, small colonies were visited twice weekly, while old, large colonies were visited only once per week. It might, therefore, be suggested that the greater output of the small colonies was somehow due to the more frequent research disturbance. Parsons and Burger (1982) reported that frequently disturbed nestling Black-crowned Night Herons (*Nycticorax nycticorax*) habituated to human visitors and were less likely to flee their nest than undisturbed nestlings. They suggested that this habituation may have increased the probability of fledging and survival. Robert and Ralph (1975) found that while egg loss increased with the frequency of disturbance on a Western Gull (*L. occidentallis*) colony, chick survival was greater at more frequently disturbed sites. These authors also attributed the higher chick survival to habituation. Frequently disturbed chicks were less frightened and less subject to attack by adults on adjacent territories.

Although this mechanism may have had a small impact on my study colonies, young cormorants do not typically leave their nests until approximately 18 to 21 days of age. By this age they are not subject to gull predation, and are fully capable of returning to the nest and/or finding their parent(s) for feeding. Although adjacent adults may be intolerant to wandering young, territories are beginning to break down by this time and young are seldom if ever harmed (Mendall 1936). There is little reason to suspect that increased habituation of chicks to more frequent visits could have resulted in the greater output from these colonies.

Several authors have found that late nesting is inhibited or decreased on frequently disturbed colonies (Ellison and Cleary 1978, Tremblay and Ellison 1979). In my study, late nests and renests were both more abundant on old, large, less disturbed colonies. This may have increased the relative output of smaller colonies in two ways. If disturbance prevents or decreases late nesting, then small colonies would become relatively more synchronous and then possibly, therefore, more productive and successful. In addition, if cormorants that nest later are younger, less productive and/or less successful breeders, then their abundance on old large colonies may have decreased the overall reproductive output. Additional study of a known aged population will be required before the relative impact of this factor is defined.

Nest Site Selection: Central vs. Peripheral

The reproductive consequences of variations in nest site parameters has been an active area of colonial waterbird research. Of all the parameters examined, the difference between centrally and peripherally located nests has been most often compared. Coulson (1968) reported that Kittiwakes nesting in the center of a colony exhibited lower annual mortality and better reproductive success than similar birds on the periphery. Similar preferential success of central nesting individuals has subsequently been reported by Tenaza (1971) for Adelie Penguins (*Pygoscelis adeliae*), by Dexheimer and Southern (1974) for Ring-billed Gulls, and by Gochfeld (1980) for Magellanic Penguins (*Spheniscus magellanicus*). Other researchers have found no significant differences in productivity between central and peripheral sites (Knopf 1979, Ryder and Ryder 1981).

One or both of two general mechanisms are usually invoked to explain the preferential success of central over peripheral nest sites. The differences may be due to inherent differences in habitat quality (i.e., exposure to predators, disturbance or habitat destruction), or to the fact that young breeders, which are less successful wherever they nest, may be selectively concentrated in peripheral sites, thus reducing the reproductive success or output of these nests.

No detailed comparison of reproductive parameters between central and peripheral nesting Double-crested Cormorants has been published. Siegel-Causey and Hunt (1981), however, found that aerial predators visited peripheral cormorant nests more often than central sites, and had significantly greater per visit success at peripheral nests.

In southern Alberta, I found that breeding cormorants clearly preferred central nest sites. Once established, centrally located breeders fledged more young per nest than those at peripheral sites. Although central nests lost significantly more eggs prior to clutch completion, slightly greater hatching and fledging success resulted in significantly greater nest success, thus producing more young per nest.

The reasons behind this disparity are not clear. Although the comparative age of breeders is not known, clutch size in central and peripheral nests was virtually identical. If Double-crested Cormorants follow the general trend towards increasing clutch size with increasing age (Lack 1968, Van de Veen 1973, Hogan 1979), this would suggest that the age composition at these sites was not significantly different. The fact that central nesting pairs layed more total eggs to attain an equivalent clutch size, however, confuses this relationship, and suggests that females occupying central sites may be more persistent or able breeders.

The differential effects of inherent habitat values between these two nest types are similarly difficult to document. If peripheral nests are more subject to predation, either because their occupants are less attentive (younger), or because their location does not afford equivalent protection from adjacent nests (Tenaza 1971), then losses to predation at these sites should be more frequent. In fact, known egg predation was slightly, but not significantly, more frequent at central nests. Even if all the eggs which disappeared are assumed to have been taken by predators, the difference in predation pressure was not significant between central and peripheral sites (Chi^2 p = 0.1421).

While it was not possible to document the fate of individual chicks, the majority of post hatching loss was due to chicks disappearing from the nest. Much of this disappearance, particularly during the first 10-14 days after hatching, was probably due to predation. After this age, chicks are not generally vulnerable to avian predators and before this age, young will not usually leave their nest. As central nests lose proportionally fewer young than peripheral nests, habitat influenced predation may contribute to the decreased success of peripheral nests.

The growth and survival curves of individuals within a brood are presented in Figure 21. These curves suggest that sibling competition or harassment may also reduce brood size. Although habitat values may not directly influence sibling survival, experienced pairs may be both more able to compete for 'prime' central locations, and better able to breed and care for larger broods. Tenaza (1971) suggested that Adelie penguins which nest in central locations have stronger incubation tendencies and Coulson and White (1958) suggested that lower breeding success in younger Kittiwakes may be due to inadequate incubation behavior or reduced ability to care for chicks. If younger cormorants returned later and were less able to obtain or keep a central nest site, then the lower reproductive parameters observed at peripheral nest sites may have been due to a combination of both age and habitat related factors.

Nest Site Selection: nest height and age

I examined two additional nest site parameters which have not previously been studied in ground nesting Double-crested Cormorants: nest height and nest age. In southern Alberta, these two factors are clearly interrelated. Most active nest structures persist from one year to the next, increasing in height with age and repeated use (Figure

25). This may be due to climatic conditions favoring the preservation of nesting platforms as suggested by Vermeer (1970c). It is, however, also true that the colony islands are high enough not to be scoured by ice each year. On several low lying colonies in northern Alberta, nests are often destroyed in early spring by ice scouring the top of colony islands.

Nests which fail during their first year of use are often abandoned and totally dismantled by cormorants removing the nest materials. Normally, however, a nest which has been active for one or two years has grown to such an extent that even if it is abandoned during a single season it is not entirely destroyed. New or loose nest material will be removed, but a basal mound of partially decomposed material will remain to mark the used site. Even this remnant, however, may disappear if it is not reused in subsequent years.

In contrast, nests which are reused in several subsequent seasons tend to increase in height. Although the height of an individual nest seldom reaches beyond 50 cm, the core area of an old colony such as Lake Newell, is supported by a broad mound of decomposing nest material and guano. Recent nests may, therefore, be more than 1 m above the original island top.

The presence of a large nest structure in spring indicates a site which has been used, probably successfully, for several years. In view of this relationship, I suspected that a breeding cormorant could enhance his reproductive chances by choosing to reuse a previously built nest rather than risk colonizing new habitat. A cormorant which returned early and had a wide variety of reused sites to choose from might further enhance his chances by selecting a taller nest over a lower, younger and less proven site. Similarly, a female might benefit by choosing a male courting on a tall, reused nest over one occupying a low, new site.

Other factors may also contribute to a preference for previously used structures. Thompson (1981) suggested that Double-crested Cormorants utilizing vacant Great Blue Heron (*Ardea herodias*) nests in Montana may have obtained an advantage by reducing the amount of time and energy required for nest construction thereby allowing early nest initiation. As both reproductive success and output decline over the season, quick nest initiation may provide significant reproductive advantage. This may become increasingly important as the breeding season becomes truncated in northern areas.

In southern Alberta, Double-crested Cormorants clearly preferred to occupy previously built nests rather than building at new sites. The mean nest initiation date was almost 10 days earlier at reused sites (Table 14). The reproductive output of pairs reusing previously built nests was also slightly higher than those nesting at new sites. Only the total number of eggs and clutch size were significantly greater however, and reproductive success was very similar between the two groups. It appeared that little obvious benefit was gained by simply reusing a previously built nest site.

When reused nests were separated into those used for the second time and those used for the third or greater time, a much stronger relationship was apparent (Table 15). Nests used for the third or greater time were significantly more productive than either new or two year old nests. They also had significantly greater fledging and overall nest success than either of the newer nest categories. There was however, no significant difference in reproductive parameters between new nests and those used for only the second time.

An explanation of this increase in reproductive output and success at frequently used sites relies on several factors. These nests are occupied earlier than either new or second use sites, probably by older, more experienced birds. If reproductive output increases with age and/or experience, then the observed increase in reproductive output and success at these sites will be partially due to differences in the quality of the breeders occupying these sites.

The location and size of the nest itself may also benefit the occupants. As we have seen, nest height increases with nest age and the tallest nests are more successful than medium or low ones (Table 13). In addition central nests are significantly more productive and successful than those located peripherally. Nests occupied for three or more years are significantly taller than either new nests or nests used for a second time. They are also most often located at central sites; significantly more often than new nests and numerically more often than nests used for a second time (Table 15). It may be that these taller more central nests are easier to defend from conspecifics or predators, or that they take less time and energy to prepare for laying, or possibly that the occupants of these sites receive greater 'social stimulation' and therefore reproduce more rapidly or successfully. Whatever the reason, the physical characteristics of frequently used nests show a consistent interrelated pattern which undoubtedly contributes to the greater reproductive parameters of birds occupying them.

A third factor which may also contribute to this pattern is the possible increase in reproductive success in pairs which stay together for several years. Coulson (1966) found that in Kittiwakes, reproductive success was higher in pairs which had previously bred successfully; and that although nest site fidelity was high, nests which failed were more likely to be abandoned in subsequent years than successful sites.

If cormorants maintain a pair bond between years, if these pairs tend to return to the same nest sites, and if experienced pairs are more successful than newly formed pairs then nest sites which have been reused for several years would be expected to be more successful than those which have been more recently established. Clearly, however, much additional data on mate and nest site fidelity are necessary before this relationship can be verified.

Although high nests and nests used for 3 or more years are significantly more successful than their lower, more recent counterparts, no similar differences were found between low vs. medium or new vs. second use nests. The fact that no significant difference was found in any measure of reproductive output or success between these categories suggests that the reproductive advantage of occupying older and/or taller nests is not sufficient to alter mean reproductive parameters until the nest becomes more than 30 cm tall or 3+ years old.

VI. Future Research Directions

A large portion of my reason for initiating this study was to provide a data base from which rational management decisions could be made regarding Double-crested Cormorants in particular, and colonial nesting birds in general. Although this document provides a first step in this direction, many additional questions remain to be answered. Most pertinent among these, I believe, is the documentation of intercolony dynamics. What is the relative importance of different colonies and colony types to the Alberta population? In order to address this topic it will be necessary to document the colony and nest site fidelity and reproductive parameters of individually marked birds.

Although I have addressed several general aspects of the effects of and the reaction to human disturbance at nesting colonies, more detailed work is also required in this area. The documentation of thermal tolerances, parental behavior and age specific reactions to disturbance will be particularly important.

In order to more clearly understand the population dynamics of this species in Alberta, it will be necessary to examine the reproductive output and success of known-aged birds through several seasons. This data, combined with the extensive banding program which has been carried out in Alberta since 1977, will allow the production of a detailed life history and demography of the Alberta population. This data could also be applied to the question of colony dynamics.

As human popualtion densities increase and land use intensifies, it will become increasingly important to understand the processes controlling colony initiation and habitat selection. The relatively complete history of southern Alberta colonies and the rapid expansion of this population provide an excellent opportunity for examining this question. Some of the factors influencing nest site selection were addressed in this study, and some additional information has already been collected on the effects of colony site modification (Anderson 1982, W. Van Schick pers. comm.). From my experience in southern Alberta, I would suggest that Double-crested Cormorants tend to follow other colonial species (gulls, herons) into new breeding habitat, but this hypothesis remains to be tested.

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